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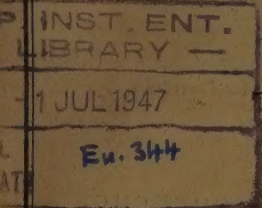
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EXPERIMENTS IN THE HYBRIDISATION OF TSETSE-FLIES (*GLOSSINA*, *DIPTERA*) AND THE POSSIBILITY OF A NEW METHOD OF CONTROL

By F. L. VANDERPLANK

(Entomologist, Tsetse Research Department, Tanganyika)

Manuscript received 8th July, 1946.

(Read 6th November, 1946)

WITH 2 PLATES.

INTRODUCTION.

HYBRIDISATION of *Glossina morsitans* Westwood, *G. swynnertoni* Austen and *G. pallidipes* Austen was attempted in order to discover—

- (a) Whether the three could be regarded as distinct species or as sub-species of *morsitans* ;
- (b) Whether they would mate freely with one another, and if not by what means the three closely allied forms distinguished their own kind ;
- (c) Whether *morsitans* and *swynnertoni* would readily produce hybrid offspring, and if so, what proportion of females would do so, and what proportion of hybrids would be sterile ;
- (d) Finally, whether interference with one species by another could be used as a measure of control.

I also wanted to explore other details including markings, colouration and nature of the genitalia of the hybrids, and whether these characters were constant or variable.

Some previous work had already been done on this subject. Corson (1932) crossed 12 female *morsitans* with male *swynnertoni*. Though the females lived from 43 to 70 days, and no more than 20 to 25 days at those temperatures was needed for production of the first larvae, only 2 (17 per cent.) of his females gave birth, and then only to 3 larvae in all (0.25 per female). Corson's 3 hybrid pupae emerged as females which he states were like *morsitans*, and he suggests that they were produced parthenogenetically : Potts (1936, unpublished) has done quite extensive work, originally undertaken to find whether sterile hybrids were produced freely enough to offer means of control, but had given up the idea since he considered the hybrids were fertile. He had kept the majority of his hybrids and has since examined them and compared them with those obtained in the present experiments. Unfortunately, however, the offspring from both types of female hybrids back-crossed with male *swynnertoni* and male *morsitans* ; all those of which specimens still remain are females in which sex the genitalia have no diagnostic value.

Certain results have been reported in full in appendices which are filed in typescript in the Tsetse Research Department, Tanganyika, and in the London School of Hygiene and Tropical Medicine.

METHODS USED IN PRESENT INVESTIGATION.

(a) Three different techniques were used. The main technique, to determine longevity and productivity, may be called the single tube method. Each tsetse as it emerges from its isolated pupa is placed in a 3×1 inch glass tube with one end corked and the other covered with cotton gauze, mesh 100 per sq. cm. Flies emerging from large collections of pupae were isolated immediately on emergence, and similarly treated. The tube was numbered and the data are recorded on a card index filing system, duplicated in a foolscap book in which data of meals taken are also noted. Although in East Africa it is often the practice to leave work of this nature to African assistants, I have carried out myself all the work on these flies except the routine feeding. In this way, the age of the fly, its source as a pupa, and (if a female) whether or not it has been in copulation, are known with certainty.

The tubes were kept gauze downwards on calico-covered wire gauze over a tray of water, contained in a large box kept shut most of the time. It has been found that flies lived better at a high humidity and in a dim light or darkness; bright light increased activity and injury in the tubes.

The flies were mated individually and observed by myself. Later as pupae appeared, these were recorded and removed under my supervision. The gauze covering the bottom of the tube was too fine to allow even a small larva to squeeze through. When a female died, it was recorded and dissected by an African assistant, and the dissection was checked by me, or by Mr. W. H. Potts (Senior Entomologist) on occasions when I was away. A few of the flies which died after feeding would not be discovered until the following morning, and then would be too rotten for dissection owing to rapid putrefaction of the blood-meal. The tubes after 3 or 4 weeks became fouled, and in order to avoid mistakes I undertook all changing of flies into clean tubes.

(b) The second method, used to obtain large numbers of hybrids and laboratory bred flies, was to keep males and females of alternate species in "Bruce"¹ boxes. All the females were dissected on death and the genitalia of the males were examined. This work was carried out by the head African laboratory assistant, and since the hybrids were wanted only for genitalia examination an error would not have had serious consequences. In fact no errors were made and all pupae that emerged as males were found to be true hybrids; it will be noted that the females of these closely related insects cannot be identified by the genitalia.

(c) The third method used was designed to study the mating of different species. Flies were introduced into a cage $30 \times 30 \times 30$ cm., with cellophane on three sides and bottom, and cotton mosquito netting on the top and remaining side, which was provided with a sleeve for insertion and removal of flies. Sometimes males of two species were introduced first, and virgin females of the same two species were mixed and added later; at other times the procedure was reversed. The

¹ A "Bruce" box is a small gauze-covered box, similar to those described and used by Bruce in his work.

copulating pairs were taken out by hand, and the genitalia of the males and the spermathecae and ovaries of the females were examined. A few females were kept alive singly in tubes as already described.

RESULTS.

General remarks.

The single tube method gives excellent mean longevity. Table 1 shows the mean life of *morsitans* and *swynnertoni* (excluding any intentionally or accidentally killed) and distinguishes those mated with

TABLE 1.

Mean life of females used in interspecific and intraspecific matings, excluding those killed or escaped.

Species	INTERSPECIFIC		INTRASPECIFIC (Controls)	
	Number	Mean life (days)	Number	Mean life (days)
<i>G. swynnertoni</i> females	72	75.6	27	58.4
<i>G. morsitans</i> females	58	81.5	34	80.0
<i>G. morsitans</i> and <i>G. swynnertoni</i> females mated and inseminated by male <i>G. pallidipes</i>	4	81.7		

There is no significant difference by Student's *t* test either between longevity of interspecific and intraspecific matings or between *G. swynnertoni* and *G. morsitans*.

another species ("interspecific") and those mated with their own ("intra-specific controls"). There are no significant differences by Student's *t* test, between intraspecifically and interspecifically mated females, or between *morsitans* and *swynnertoni*. Longevity varied between a few hours and 160 days. Jack (1939) and Potts (unpublished) have kept a few *morsitans* alive longer in captivity; Jack records one living 233 days and Potts had several living over 180 days, but not as long as 190 days.

A total of 92 virgin *swynnertoni* were mated with male *morsitans* and a further 48 with their own species; 82 virgin *morsitans* were mated with male *swynnertoni* and 37 with their own species. Some of these figures are higher than those given in Table 1, because some individuals which were killed or escaped are excluded from the table. In addition, one virgin *morsitans* and 4 virgin *swynnertoni* were mated with male *pallidipes*, but insemination by this species did not occur except with one *swynnertoni* after an hour. The *morsitans* copulation lasted twenty minutes.

Previous unpublished work by me has shown that virgin females of these species are always attractive to males of their own kind, and do not, as Mellanby (1937) suggests for *G. palpalis fuscipes*, become more attractive about the seventh to tenth day. However, the females of *morsitans*, *swynnertoni* and *pallidipes* always appear to resist the attentions of the male when they are able to do so, but they are unable to bend their abdomens sufficiently to prevent coitus (*a*) in the first hour

after emergence and (b) when fully engorged after the first or a subsequent meal. It is at these two periods that copulation takes place most readily in captivity, and dissections of over 10,000 wild *swynnertoni* and over 2,000 wild *pallidipes* show that approximately one-third of the teneral² females (which have not yet taken their first meal) are inseminated, whereas all the non-teneral females are found to have been inseminated. Further, all copulations hitherto observed in the field are with teneral females.

A female 24 to 48 hours after insemination is generally no longer attractive to males, and even should it be attempted she will resist coitus. After a meal the female is unable to resist successfully, but if a male is induced to copulate the act lasts only a few minutes and it is doubtful if any sperm is passed. Various authors have suggested that *Glossina* females lead a retired life in the field in order to avoid the males, but it is suggested that once a female has been inseminated she has no need for activities other than the search for food and devotes the rest of her life to producing larvae.

Mellanby (1937) states that the ova of *palpalis* are unable to pass down from the ovaries through the oviducts to the uterus unless the female has previously been inseminated. This does not appear to be so in the species studied here, except in a few pathological cases, where probably because of insufficient feeding or exercise in captivity the eggs do actually pile up in the ovaries. In at least 20 virgin *morsitans*, *swynnertoni* and *pallidipes*, and 10 virgin *palpalis fuscipes* dissected when between 30 and 90 days old, the eggs had passed down normally. Since it has been found (Mellanby, 1937) and confirmed that the right ovary develops first, it is quite easy to ascertain that at least one egg has been extruded, and that non-insemination has not inhibited further development of the ovaries. However, non-insemination may delay ovulation. At the temperatures obtaining, 21°C.-23°C., the first ovulation would be expected about the 12th to 13th day, but in virgin females it is often delayed until the 20th to 22nd day. A further account of the development of the ovaries will be given elsewhere.

Insemination.

Only flies whose spermathecae were examined, or which had produced larvae, are included in Table 2. As noted above, not all the dead individuals could be dissected, because of putrefaction, and this fact introduces a slight bias, because some unproductive interspecific individuals must have been excluded although inseminated.

Table 2 shows the numbers of *morsitans* and *swynnertoni* dissected, whether after natural death or intentionally killed, and compares inseminated interspecific females with intraspecific controls. Although only flies which had been in copulation at least two hours are included, some females in both interspecific and intraspecific groups failed to

² Teneral is the word used for flies with unhardened chitin. The chitin does not become hard until after the first meal of blood, which is normally taken about three days after emergence.

become inseminated. (In each species it happens that the percentage not inseminated is insignificantly higher in the intraspecific than in the interspecific series.)

Production of Pupae.

Table 3 summarises the number of individual females that produced one or more pupae, compared with the number that were fully inseminated and had lived at least 21 days. The intraspecific controls were treated in exactly the same way as the interspecifically mated females. They were randomised with each other and the assistants feeding the flies had no means of knowing which were controls and which were not, since the individuals were known to them by numbers only in the whole series spread over nine months.

Sixty to 90 per cent. of the females in the intraspecific controls of both species produced at least one pupa, whereas only 5 pupae resulted from 80 *swynnertoni* females crossed with *morsitans*, and only 14 from 59 female *morsitans* crossed with *swynnertoni*. By χ_c the differences in fertility between intraspecific and interspecific matings are significant.

Table 4 summarises the actual numbers of pupae produced. The controls produced several times as many pupae as the interspecifically mated females, the difference being significant by χ_c . (The *morsitans* controls produced 3 pupae per female, which, though probably one of the highest means recorded, is less than the expectation of 6 with regular births, doubtless because a lack of sufficiently large meals at the right time results in premature birth or complete abortion.)

Mating Experiments.

In the first experiment 15 male *swynnertoni* and 15 male *morsitans* at least 7 days old were placed in the mating cage described above, and a jar containing emerging female *swynnertoni* was added. The 23 copulating pairs were removed, when it was found (Table 5) that the copulating males included 13 *swynnertoni* and 10 *morsitans*.

Later 6 experiments were done at different times and under different conditions. Experiment No. 3 (Table 6) is typical. Male *morsitans* and *swynnertoni*, 15 of each, were placed in the cage and allowed to mix. All were at least 13 days old. 10 virgin females of each species one day old were offered a meal, mixed in a tube, and released all together in the cage. The 18 pairs removed were kept until coitus was complete. Most were then dissected at once and a few were dissected when they died naturally. Naming the males first in the couplings, the result was 4 *morsitans-morsitans*, 3 *swynnertoni-swynnertoni*, 5 *morsitans-swynnertoni* and 6 *swynnertoni-morsitans*. Although all were observed in copulation for over two hours, 3 *swynnertoni-morsitans* couplings failed to result in insemination. All the rest were found fully inseminated except one that was too putrefied to dissect.

The results of the 6 experiments are summarised in Table 7. The slight bias in favour of intraspecific matings is insignificant, and as far as these data go mating between individuals of these two species appears to be not specific but random.

TABLE 2.

Comparison of those inseminated and those not inseminated in both interspecific and intraspecific (control) matings. All had been observed in coitus for at least 2 hours.

Species (female)	INTERSPECIFIC			INTRASPECIFIC (Controls)		
	Number inseminated	Number not inseminated	Per cent. not inseminated	Number inseminated	Number not insem.	Per cent. not inseminated
<i>G. swynnertoni</i>	92	8	8.0	48	12	20.0
<i>G. morsitans</i>	82	9	9.9	37	12	24.5

TABLE 3.

Showing the number of females of both species mated interspecifically and intraspecifically that were fully inseminated and survived 21 days (time required at the prevailing temperatures to produce first pupa), and that produced one or more pupae.

Species (female)	INTERSPECIFIC			INTRASPECIFIC (Controls)			DIFF. $\bar{X}^2$
	Number insem.	Number that produced	Per cent.	Number insem.	Number that produced	Per cent.	
<i>G. swynnertoni</i>	80	5	6.3	27	16	59.3	45.2
<i>G. morsitans</i>	59	14	23.7	34	33	97.0	46.3

DIFF. $\bar{X}^2$

8.8 sig.

13.6 sig.

TABLE 4.

Showing the number of pupae per female, excluding premature or aborted larvae, from both interspecific and intraspecific (control) matings.

Species	INTERSPECIFIC			INTRASPECIFIC (Controls)		
	Number of inseminated females	Total pupae	Pupae per female	Number of inseminated females	Total pupae	Pupae per female
<i>G. swynnertoni</i>	80	5	0.063	27	29	1.07
<i>G. morsitans</i>	59	21	0.356	34	103	3.03

Two further experiments included *pallidipes*. Although the males of this species considerably exceeded the females, they did not attempt to mate with either *morsitans* or *swynnertoni*; and though a few of these two species did attempt to mate with *pallidipes* females no successful copulation was observed.

In another experiment male *morsitans* and *swynnertoni* were individually marked and numbered, then introduced to females of each species. After a few days they were used for a similar experiment, when it was found that all which had effected respectively intraspecific or interspecific couplings on the first occasion did so again on the second, with the single exception of one *swynnertoni* intraspecifically mated the first time and mated with a *morsitans* on the second.

Appearance of Hybrids.

The male and female hybrids from crosses of both *morsitans-swynnertoni* and *swynnertoni-morsitans* were all externally identical with wild *swynnertoni* from the Shinyanga area, the most careful examination failing to discover any distinction. Corson (1932), as already mentioned, stated that his hybrids were like *morsitans*. It is suggested that he may have examined them soon after emergence when it is normal for even pure-bred *swynnertoni* to have light banding recalling that of *morsitans*: the young flies darken within 24 hours of emergence, but if killed immediately they fail to do so and their banding remains light and irregular like that of *morsitans*.

Although the external appearance of the hybrid gives no clue to its identity, examination of the male genitalia is conclusive.

TABLE 5.
Mating Experiment.

Order of copulation	Species of MALE	Species of FEMALE teneral virgins	Whether inseminated	Notes
1	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
2	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
3	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	I	Not kept.
4	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	I	Not kept.
5	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
6	<i>G. morsitans</i>	<i>G. swynnertoni</i>	?	Not dissected. Failed to reproduce.
7	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	Not I	Not kept.
8	<i>G. morsitans</i>	<i>G. swynnertoni</i>	Not I	Not kept.
9	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
10	<i>G. morsitans</i>	<i>G. swynnertoni</i>	Not I	Not kept.
11	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
12	<i>G. morsitans</i>	<i>G. swynnertoni</i>	?	Not dissected. Failed to reproduce. Died aged 89 days.
13	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	Not I	Not kept.
14	<i>G. morsitans</i>	<i>G. swynnertoni</i>	?	Not dissected. Failed to reproduce. Died aged 148 days.
15	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
16	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
17	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	FI	Not kept.
18	<i>G. morsitans</i>	<i>G. swynnertoni</i>	FI	Failed to reproduce. Died aged 64 days.
19	<i>G. morsitans</i>	<i>G. swynnertoni</i>	Not I	Not kept.
20	<i>G. morsitans</i>	<i>G. swynnertoni</i>	Not I	Not kept.
21	<i>G. swynnertoni</i>	<i>G. swynnertoni</i>	Not I	Not kept.
22	<i>G. morsitans</i>	<i>G. swynnertoni</i>	I	Not kept.
23	<i>G. morsitans</i>	<i>G. swynnertoni</i>	FI	Not kept.

I = Inseminated.

FI = Fully Inseminated.

Fig. 1 (Plate 1) shows the typical male genitalia of *morsitans* from Kondoa Irangi, Central Tanganyika, whence the experimental pupae came. Some 500 adult males taken at different seasons have so far been examined from this area, and although there is a certain amount of variation in absolute size, due to seasonal trends, there is no detectable variation in the relative proportions of the different structures. So far I have prepared, mounted and examined male genitalia of some 3,500

TABLE 6.
Mating Experiment No. 3.

Order of copulation	MALE	FEMALE	Time of copulation	Time finished	Whether inseminated or not	Notes
1	<i>G. morsitans</i>	<i>G. morsitans</i>	12.0	8.30 a.m.	FI	Not kept.
2	<i>G. swynnertonii</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	FI	Produced 1 pupa. ♀. Died aged 41 days.
3	<i>G. morsitans</i>	<i>G. morsitans</i>	12.0	5.00 plus	FI/	Produced 5 pupae. ♀♂♀♂. Died aged 97 days.
4	<i>G. swynnertonii</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	Not I	Died aged 80 days.
5	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	FI	Failed to reproduce. Died aged 108 days.
6	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	—	Not dissected. Failed to reproduce. Died aged 135 days.
7	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	4.30 plus	FI	Not kept.
8	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	FI	Too young to reproduce. Died aged 16 days.
9	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.0	4.30	FI	Not kept.
10	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.0	5.00 plus	I	Failed to reproduce. Died aged 122 days.
11	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.0	2.00	Not I	Not kept.
12	<i>G. morsitans</i>	<i>G. morsitans</i>	12.0	2.00	FI	Not kept.
13	<i>G. swynnertonii</i>	<i>G. swynnertonii</i>	12.0	4.30	FI	Not kept.
14	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	FI	Failed to reproduce. Died aged 119 days.
15	<i>G. morsitans</i>	<i>G. swynnertonii</i>	12.0	5.00 plus	FI	Failed to reproduce. Died aged 67 days.
16	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.0	5.00 plus	Not I	Not kept.
17	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.15	5.00 plus	FI	Failed to reproduce. Died aged 58 days.
18	<i>G. swynnertonii</i>	<i>G. morsitans</i>	12.30	5.00 plus	Not I	Not kept.

Fifteen male *G. morsitans* and *G. swynnertonii* at least 13 days old were allowed to mix in mating cage; later a mixed batch of ten gorged virgin female *morsitans* with similarly ten *swynnertonii* were introduced. The resulting copulations are tabulated above.

TABLE 7.

Experiment		No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	Total
♂	♀							
<i>G. morsitans</i>	× <i>G. morsitans</i>	4	4	7	2	10	1	28
<i>G. swynnertoni</i>	× <i>G. swynnertoni</i>	5	3	7	3	7	2	27
<i>G. morsitans</i>	× <i>G. swynnertoni</i>	3	5	4	1	7	2	22
<i>G. swynnertoni</i>	× <i>G. morsitans</i>	3	6	7	1	5	2	24
		15	18	25	7	29	7	101

morsitans from over fifty localities in Tanganyika, Northern and Southern Rhodesia, Nyasaland, Portuguese East Africa, Uganda, Bechuanaland, Belgian Congo, Nigeria and Gambia. These can be divided into distinct types (including *G. sub-morsitans* as one type) which merge into each other, but no abnormalities have been encountered except in three areas where *morsitans* borders on *swynnertoni* country and a mixed belt occurs. (See W. H. Potts for a description of two of these areas in the Appendix.)

Although Newstead, Evans and Potts (1924) and Patton (1936) have described these species carefully, it is thought advisable to note the salient points which affect the present comparisons. The superior claspers (*Sc*) are rounded and waisted in contrast to those of *swynnertoni* (fig. 2, Plate 1), which are broad and straighter along their outer margins. The rudimentary claw (*rc*) is less prominent in *morsitans*. But the most striking difference is in the median lobes (*ml*) which in flattened *morsitans* preparations project at least to the level of the superior claspers, with their apices (*ap*) or "feet" turned sharply outwards. (In the live fly the "feet" are directed in a morphologically ventral direction and serve as a claw.) The bases of the median lobes are short and are cut away to join the inner sides of the superior claspers, instead of being continued into submedian right-angled plates (*sp*) as in *swynnertoni*, in which species furthermore the median lobes are narrow and pointed and lack the *morsitans* "foot." (In the Konda Irangi *morsitans*, the "foot" has no marked "heel" or inner projection and does not, as in *morsitans* elsewhere, project beyond the superior claspers.)

Fig. 2 (Plate 1) shows typical male genitalia of *swynnertoni*, one of 1,500 permanent preparations from the Shinyanga area, whence the pupae for these experiments were obtained. A further 1,500 permanent preparations of *swynnertoni* from various other localities were examined but no measurable variations or abnormalities were found except, as mentioned above, for *morsitans*, in three areas where *morsitans* and *swynnertoni* overlap. The median lobes are always narrow and pointed, some very short, others projecting as far as the level of the superior claspers but not beyond. As already mentioned, the semi-chitinated basal portion continued submedially as a right-angled plate, which is prolonged on its outer side right along the inner margin of the superior claspers. In 3,000 *swynnertoni* from Shinyanga, Arusha and Musoma districts, the median lobes are always pointed, often tapering and pointed.

Fig. 3 (Plate 1) shows typical genitalia of a hybrid "*morsitoni*" resulting from crossing a *morsitans* male with a *swynnertoni* female. The superior claspers are *swynnertoni*-like, but the median lobes are broader than in *swynnertoni*, project further and are blunt-ended. Also, instead of the basal semi-chitinated plate with a right-angled inner corner, the base is rounded and follows parallel with the inner curve of the superior clasper rather as in *submorsitans*. The genitalia are distinctive and cannot be confused with typical or even atypical *morsitans*, *submorsitans* or *swynnertoni*. Ten specimens have been examined, and the only material variation noted is in the comparative length of the median lobes.

Fig. 4 (Plate 1) shows typical genitalia of a male hybrid "*swynnertans*" from male *swynnertoni* and female *morsitans* parents. The rudimentary claw is prominent as it usually is in *swynnertoni*. The median lobes are broader than in typical *swynnertoni*, but not as broad as in typical *morsitans* or *submorsitans*. Their apices are not turned outwards, that is, there are no "feet," but each lobe is cut off diagonally at its end, with the sharp angle on the outer side rather as if the "feet" had been straightened out. The semi-chitinated base is prolonged to follow parallel with the inner side of the superior clasper. This description is typical of some 50 hybrids examined so far.

Newstead's original drawing (1910) of the male genitalia of *morsitans* and *submorsitans* illustrates clearly the points mentioned, but Patton's (1936) illustrations are indistinct and fail to show them.

ATTEMPTS TO BREED FROM THE *GLOSSINA* HYBRIDS AND COMPARISON WITH RESULTS FROM FIRST FILIAL GENERATION LABORATORY-BRED CONTROLS.

Table 8 gives the mean weights of hybrid and control pupae. All are smaller than those from the field, but by "Student's" *t* test there is no significant difference between the means of hybrids and controls. However, as is usual with laboratory-bred *Glossina*, many of the emerging imagines were considerably underweight and undersized; these were killed and not used for hybrid matings. Lack of staff—it required five assistants to maintain 150 single tubes—also limited the total number of experiments that could be attempted, but the results tend to show that the hybrids are at least partly sterile, which would be in line with experiments on other Diptera, notably *Drosophila*.

Two types of hybrids were tried, *morsitoni* and *swynnertans*. The parents of *morsitoni* were male *morsitans* and female *swynnertoni*, and of *swynnertans* male *swynnertoni* and female *morsitans*. Single male hybrids mated with several different females; for example, the male hybrid "*swynnertans* B4" was mated at various times with 3 *morsitans*, 2 *swynnertans* and 4 *swynnertoni*—none of which produced any offspring. Full details of all these matings are deposited with the Tsetse Research Department, Tanganyika.

Table 9 compares the longevity of the females of each separate batch of matings, because mean life is an index of the success of laboratory treatment. Female hybrids appear (on small numbers) to live longer than controls, possibly because the small individuals were rejected as

TABLE 8.
Weights (mg.) of puparia of species and hybrids of *Glossina*.

	<i>morsitans</i>		" <i>morsitoni</i> "	" <i>swynnertans</i> "	<i>swynnertoni</i>	
	P.	F ₁	F ₁	F ₁	P.	F ₁
Number	39	1	9	34	19	3
Mean weight	21.2	16.5	20.5	21.4	22.9	22.3

TABLE 9.

Mean life of females used in *hybrid* crosses and first generation controls, excluding those killed or escaped, but including those not inseminated and those not dissected.

Species of Female mated with—					Number used	Mean life (days)
<i>G. swynnertoni</i>	×	♂	hybrids		16	64.7
<i>G. morsitans</i>	×	♂	hybrids		13	75.8
hybrids	×	♂	hybrids		6	132.3
hybrids	×	♂	<i>G. swynnertoni</i>		3	71.3
and	×	♂	<i>G. morsitans</i>			
Controls :						
<i>G. morsitans</i>	×	♂	<i>G. morsitans</i>		1	106.0
<i>G. swynnertoni</i>	×	♂	<i>G. swynnertoni</i>		2	44.5

TABLE 10.

Comparison of those females mated that were inseminated and those not inseminated. Only flies that were dissected are included.

Species of Female mated with—					Number inseminated	Number not inseminated	Per cent. Negative
<i>G. swynnertoni</i>	×	♂	hybrids		10	2	16.7
<i>G. morsitans</i>	×	♂	hybrids		7	2	22.2
hybrid	×	♂	hybrids		5	0	—
hybrid	×	♂	<i>G. swynnertoni</i>		2	0	—
and	×	♂	<i>G. morsitans</i>				
Controls					3	0	—
Totals					27	4	

None of the above results is significantly different from those set out in Table 2.

already described. The results from the 3 pairs of controls—both males and females being offspring of the original control series—indicates no decline in fecundity, since all three females produced at least one pupa each (5 in all).

Table 10 shows the proportion inseminated, which is not significantly different from that in Table 2, although 7 flies (5 inseminated) are included which had not been observed in coitus for two hours.

Not one of the hybrids produced a larva, none was observed to abort, and none contained a larva when dissected. In 33 out of the 38 examined, the eggs had passed down normally into the uterus. We have already seen that all three first filial generation intraspecific controls—2 *swynnertoni* and 1 *morsitans*—had offspring.

FIELD OBSERVATIONS.

Examination of Wild *Glossina* from Areas of Mixed Species.

A sample of male *Glossina* was collected in Kondoa Irangi district, near Chungai, where the belts of *morsitans* and *swynnertoni* overlap. The banding and genitalia of these flies were examined. Of 51 flies, 17 were pure-bred *swynnertoni* and 13 pure-bred *morsitans*. One was a typical "*morsitoni*," that is, its parents were evidently a male *morsitans* and a female *swynnertoni*. The remaining 20 flies appeared to be more or less atypical *morsitans* and *swynnertoni*, and conceivably resulted from back crossing of hybrids with pure-bred flies, if indeed such is possible.

A sample of male *Glossina* was received from Babati in Mbulu district, where *morsitans*, *swynnertoni* and *pallidipes* overlap. Of 99 flies, 80 were pure-bred *morsitans* (one slightly atypical), 10 were pure-bred *swynnertoni*, 4 were typical *pallidipes* and one was evidently some kind of *pallidipes* hybrid. The genitalia from this last fly, unfortunately broken in mounting, are shown in fig. 5 (Plate 2.) It will be seen that there is a pair of processes similar to the median lobes of *swynnertoni* in the membrane between the superior claspers. Of some 600 *pallidipes* so far examined from Tanganyika and elsewhere, none has been observed with such processes. Fig. 6 (Plate 2) shows typical genitalia of *pallidipes* from the same sample, and no important differences have been detected in the specimens from elsewhere. The size and markings of the supposed hybrid were typical of *pallidipes*. A description of the Babati and Chungai areas by W. H. Potts is given in the appendix. Fig. 7 (Plate 2) shows the male genitalia of *G. longipalpis* from the Belgian Congo, a closely related species, and is included for comparison.

FIELD EXPERIMENT.

Release of *G. morsitans* in *G. swynnertoni* Bush.

Dr. C. H. N. Jackson was at this time studying the physiology of *morsitans* released in *swynnertoni* country at Shinyanga. At first young flies were allowed to emerge in the laboratory and then were marked and carried to the field, but as survival proved unsatisfactory both *morsitans* and *swynnertoni* were later allowed to emerge naturally from pupae placed in a Stevenson screen in the field for a period of ten days. Towards the end of this period, when the unmarked *morsitans* were sexually potent (5 to 7 days old), an attempt was made to observe copulating pairs in the field. Four pairs were seen—3 male *swynnertoni* with female *swynnertoni* and one male *swynnertoni* with a female *morsitans*.

Fourteen non-teneral (fed) *morsitans* females were recaptured and kept in the laboratory. Twelve lived long enough for reproduction, but only 5 actually produced pupae. One female produced 3 pupae which emerged as 2 males and a female, and examination of the male genitalia showed one to be a hybrid and the other a pure *morsitans*. It is suggested that this fly had mated with both species. Another female produced 5 pupae from which 3 male and 2 female *morsitans* emerged.

The other 3 females which had offspring produced altogether 5 pupae, of which one died and the remainder emerged as hybrids. Of the 7 females that failed to produce pupae, 3 were rotten before they could be dissected, but the other 4 were fully inseminated. No wild *swynnertoni* were kept at this time, but previous experience with some 30 non-teneral female *swynnertoni* and 20 non-teneral female *pallidipes* from the field showed that all living 20 days or more produced at least one pupa.

Two months later, 2 non-teneral female *morsitans*, evidently of the first filial generation, were captured from the neighbourhood of the release site. One died after 2 days, but the second lived 90 days, producing one pupa, which emerged as a hybrid male.

These results suggest that mating in the field between *morsitans* and *swynnertoni* is random, as indicated also by laboratory work, though there may be a tendency for the two species to become more or less segregated in different vegetational types. Also, it would appear that the numerically superior would sterilise progressively more and more of the numerically inferior species. On this basis it is hoped to make use of one species for the control of the other, since it is thought likely that, once the indigenous species is killed out, the introduced species will fail to survive indefinitely because it is not in its proper environment. Further experiments were carried out by Dr. Jackson and his results confirm the above conclusions (Jackson, 1945b).

PRACTICAL VALUE OF THE WORK.

In nature, *morsitans* and *swynnertoni* never seem to occur together in equal density, though stragglers of the one species penetrate some miles into the territory of the other. Dr. Jackson (1945) has shown that *morsitans* can survive at least in decreasing numbers, and produce a second generation, in the thornbush habitat of *swynnertoni*, and it is considered likely that the converse is true. The main problem of tsetse work is not so much to reduce a high density to a low one, as to reduce a low density to zero, and with this object 144,000 *morsitans* pupae from Kondoa Irangi were introduced into an isolated block of country, about ten square miles in area, where by other measures the density of *swynnertoni* has been brought low. The *morsitans* will probably breed to a limited extent, but it is hoped that they will ultimately die out after the introductions cease.

In some areas it might be possible to guard against replacing one species permanently by the other, by transporting live males from fly belt to fly belt, or by separating the sexes as the flies emerge from introduced pupae and releasing only males, but the advantage of breeding by the introduced species would then be lost, and more pupae would be needed to make up the numbers required.

The above field experiment attempting to eliminate *swynnertoni* by the introduction of larger numbers of *morsitans* was started in July, 1944, as a result of the laboratory work described above. The scheme for attempting to eliminate *swynnertoni* by *morsitans* can only hope to

be successful under certain given conditions, which have been described in this paper and are summarised as :—

- (a) Mating between the species must be practically at random. It has been shown to be at random in the laboratory and by Jackson (1945b) in the field.
- (b) Females only inseminated once during their lives.
- (c) Any hybrids produced must be sterile or at least nearly so, otherwise a hybrid race would replace the indigenous species.
- (d) Only the males of the introduced species must be used, unless it can be shown that the introduced species is unable to survive as an increasing population in the new environment.

In the above experiment we have proceeded on the assumption that *morsitans* will not be able to survive as an increasing population in the new environment.

It should be possible to calculate the time required for the introduced species (*morsitans*) to sterilise or hybridise out the indigenous species (*swynnertoni*). Such a calculation was made at the beginning of this field experiment, and in July, 1945, after the experiment had proceeded for twelve months, the *swynnertoni* numbers had decreased according to mathematical expectation. It is intended to publish a separate account of the details of this experiment, and the above notes are only included here to show the practical applications of the seemingly academic laboratory experiments and observations.

There are other possibilities. For example, *pallidipes* might cross easily with *longipalpis* and produce partly or completely sterile hybrids, or (as with *morsitans* and *swynnertoni*) insemination might more commonly result in no offspring at all. From laboratory experiments with *palpalis fuscipes* from Uganda and *palpalis martinii* from Lake Tanganyika it appears that mating between the two sub-species is random, but the results are not yet sufficiently known. The biological status of *submorsitans* could be determined by experiment on these lines.

SUMMARY.

1. The methods of keeping *Glossina* in captivity are described, with some observations on the development of the ovaries.

2. Crossing *Glossina morsitans* with *G. swynnertoni* generally results in insemination, but no offspring; when hybrids are produced they appear at long and irregular intervals and the males are completely sterile, the females are at least partly sterile.

3. Male *G. pallidipes* were very reluctant to mate with female *G. morsitans* and *G. swynnertoni*, and the few inseminated females had no offspring.

4. *G. morsitans* and *G. swynnertoni* appear to mate at random, but the males did not mate with the few female *G. pallidipes* tried hitherto.

5. The hybrids resulting from crossing *G. morsitans* and *G. swynnertoni* were in appearance identical with *G. swynnertoni*, which is contrary to Corson's published observation (1932). Examination of the male

genitalia of the hybrids showed that, whichever species was the male parent, the male genitalia were distinct from those of the pure-bred flies. The genitalia tend to resemble (but are distinct from) those of the maternal species.

6. The hybrids from *G. morsitans* and *G. swynnertoni* were crossed with each other and with pure-bred flies of each species. None produced a pupa, though first filial pure-bred controls produced at least one pupa each. Potts records two female hybrids crossed with *swynnertoni* and having offspring.

7. Female *G. morsitans* recovered after release (with males) in the environment of *G. swynnertoni* were kept in the laboratory. One had mated with its own species, one apparently with both, and the rest either failed to produce pupae or produced hybrids.

8. Hybrids between *G. morsitans* and *G. swynnertoni* have been found in two samples from overlapping fly belts of these species, together with a probable *G. pallidipes* hybrid.

9. It is suggested that use can be made of these results for possible extermination of an indigenous species by one introduced, provided that (as seems likely) the introduced species ultimately dies out because the habitat is not suited for its permanent survival. Other possibilities are also discussed.

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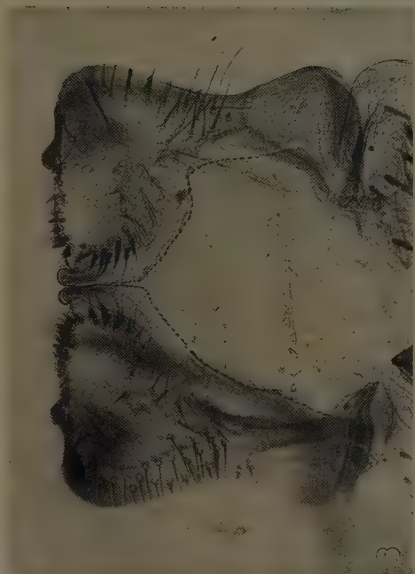
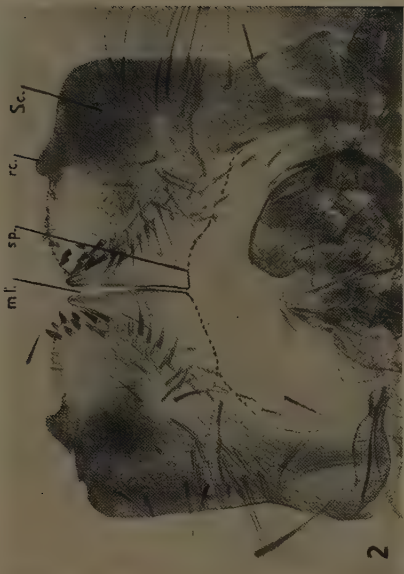
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PLATE 1.

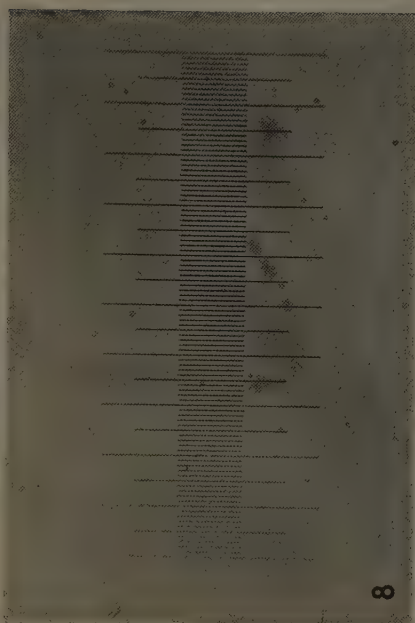
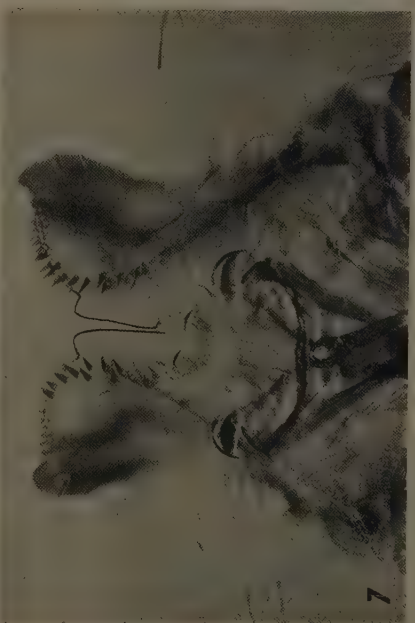
1. Typical male genitalia of *G. morsitans* from Kondoa Irangi, Tanganyika.
 2. Typical male genitalia of *G. swynnertoni* from Shinyanga, Tanganyika.
 3. Typical male genitalia of hybrid "*morsitoni*" resulting from crossing a *morsitans* male with a *swynnertoni* female.
 4. Typical male genitalia of hybrid "*swynnertans*" resulting from crossing a male *swynnertoni* with a female *morsitans*.
- Superior claspers (*Sc*), median lobes (*ml*), rudimentary claw (*rc*), apices or "feet" (*ap*), submedian right-angled plates (*sp*), "waist" (*w*).
- The photographs have been touched up to bring out certain salient points which do not show very well in the photographs although readily visible in the original material.

PLATE 2.

5. Male genitalia of atypical *G. pallidipes* or possible *pallidipes* hybrid. Broken in mounting.
6. Typical male genitalia of *G. pallidipes* from Babati, Tanganyika.
7. Male genitalia of *G. longipalpis* from the Belgian Congo.
8. Scale used for Photographs 1 to 7. Total length is equivalent to one millimetre, or each division to ten microns.



Male genitalia of species of *Glossina*.



Male genitalia of species of *Glossina*.

APPENDIX I

THE BABATI FLY AREA

BY W. H. POTTS.

The sample examined (page 12) consisted of tsetse caught at a fly picket situated near Babati, about half-way between Arusha and Dodoma on the broad North Road. These flies had been caught off traffic which had just passed through some dozen miles of the overlap of the Rift-Valley *morsitans-pallidipes* belt and the Masai *swynnertoni* belt (see Potts, 1937, Nos. 4 and 7, p. 141 and map).

Messrs. Lloyd and Du Frayer (in unpublished MSS. reports) describe five different types of woodland as composing the area concerned :—

- (i) Well-grassed woodland dominated by *Acacia spirocarpa* mostly of an open park-like nature, but in parts with a much closer stand of the component trees and a dense undergrowth containing *Harrisonia abyssinica* and *Acacia pennata* which produces a more forest-like effect; in this type *G. morsitans* occurred in fair numbers, but *G. swynnertoni* was less abundant, and indeed almost entirely absent from the denser parts.
- (ii) An open *Commiphora-Lannea* hardpan type, composed mainly of small trees of *A. schimperi* and *Lannea humilis* and widely spaced thickets of *Harrisonia abyssinica* and *Cissus* spp. Surrounding this area is a ring of country varying from dense thicket to fairly closely spaced semi-thicket clumps, dominated by the small trees *Stereospermum kunthianum* and *Euphorbia bilocularis*, with *Grewia* spp. and other thicket elements; it is this area which forms the main local centre of *G. swynnertoni*.
- (iii) Small areas of a special type of hardpan in which *Acacia kirkii* was almost the only tree present; in this tsetse were present in fairly high numbers, *G. morsitans* being the more numerous.
- (iv) Stretches of poorly drained country dominated by *Acacia xanthophloea* with dense undergrowth, and on patches comparatively better drained, *Acacia seyal*; in the latter, *G. swynnertoni* occurred in fairly low numbers, but the former was unfavourable for both species.
- (v) *Combretum* woodland, dominated by *Combretum fischeri*, with a number of other comparatively broad-leaved trees associated such as *Combretum zeyheri*, *Dalbergia melanxylon* and *Lonchocarpus* sp. and a sprinkling of fine-leaved *Acacia* (*A. benthamii* and *A. spirocarpa*) and *Dichrostachys glomerata*; this is the main stronghold of *G. morsitans*. The road passes through all the above types save (iv), the *Acacia xanthophloea* type.

The proportions in which *G. morsitans* and *G. swynnertoni* exist in their area varied, according to Mr. Lloyd (in unpublished MSS. report), in January, 1944, from approximately two *morsitans* males to one

swynnertoni male in the *Combretum* and *A. spirocarpa* woodlands to about one *morsitans* to thirteen *swynnertoni* males in the *Commiphora-Lannea* hardpan.

The preponderance of *G. morsitans* in the actual *Combretum* woodlands is, however, probably much greater than these figures show, for they came from the road, on which the numbers of *swynnertoni* would be disproportionately increased by carriage on traffic from the *swynnertoni* areas. Such an effect was recorded in the *Commiphora-Lannea* hardpan where in a catch along the road the number of *morsitans* and *swynnertoni* males approached equality, instead of showing the preponderance of *swynnertoni* quoted above; here carriage from the *morsitans* area was upsetting the balance. Mr. Du Frayer (in unpublished MSS.) recorded that off the road he took large numbers of *G. morsitans* and but few *G. swynnertoni* in the *Combretum* woodland. No reliable figures are available for the relative proportions of *G. pallidipes* in the area.

THE CHUNGAI FLY AREA.

This is an area infested with mixed *G. morsitans* and *G. swynnertoni*, formed by the overlapping of an eastern extension of the Central Province Belt of *G. morsitans* by the western edge of the Masai Belt of *G. swynnertoni* (see Potts, 1937, Nos. 5 and 7, p. 141 and map). The eastern extension of the *morsitans* belt is a narrow strip of country which lies along the foot of the miombo-clad Irangi Escarpment, and merges, through a series of transitional bush types as described by Nash, 1931, in the Kihori area, into the network of thicketed thorn bush and open grass-land which characterises the *swynnertoni*-infested eastern Masai country. The area from which the present sample of *G. morsitans* and *G. swynnertoni* came consisted of a fly round sector in which the two species were taken in the proportion of eight *morsitans* males to one *swynnertoni* male. This sector ran partly through a fairly densely treed thorn savanna in which medium sized *Acacia spirocarpa* trees dominated, with *Acacia senegal* and *Commiphora schimperi* as the other most common trees, and with thickets composed mainly of *Grewia bicolor* and *Harrisonia abyssinica*. It then ran down a narrow open grass glade, seasonally flooded, with numerous pools, but bordered by the same type of woodland on each side, and it ended at the gall acacia (*A. formicarum*) fringe of one of the big open grasslands of Masailand which have been mentioned previously.

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THE ODONATA OF THE IVORY COAST BASED ON THE MISSION OF DR. R. PAULIAN AND P. LEPESME

BY LT.-COL. F. C. FRASER, I.M.S., RETD., F.R.E.S.

Manuscript received 6th June, 1946.

(Read 6th November, 1946.)

WITH 8 TEXT-FIGURES.

It is some five years since I reported on a collection of Odonata made by Dr. R. Paulian on the West Coast of Africa (1941, *Proc. R. ent. Soc. Lond.* (B) 10 : 35); although primarily from the Cameroons, the collection contained a few species from the Ivory Coast. Now I am again indebted to him for a further and larger collection made entirely on the littoral of the Ivory Coast. In addition to a few new species, the collection has resulted in more than doubling the number of species hitherto reported from that area.

Dr. Paulian has furnished me with the following notes. "The collection comes from the 'Réserve forestière du Banco,' which is a strip of rain forest at 12 km. west of Abidjan. I have not, however, the slightest idea as to how far our collection was exhaustive: we collected all (save two) of the species we saw from the middle of June to the end of September, and *we looked for them*. Collecting was done in clearings of the forest, also along the paths and on the banks of the river Banco; a few specimens were taken at the mouth of the Banco where it runs into the lagoon."

The Odonate fauna of the Ivory Coast is not peculiar to that region, but is common to an enormous area extending from the mouth of the Senegal in the west to that of the Congo in the south, and embracing inland the whole of the catchment area drained by the three great rivers Senegal, Niger and Congo. If a map of West Africa be consulted, it will be seen how these rivers interlock, the tributaries of the Niger dovetailing into those of the Senegal westwards, whilst those of the Congo form a less intimate association with the Niger through the interposition of rivers draining into Lake Tchad. Many years spent in similar tropical country has convinced me that the distribution of most Odonata is through the medium of water-courses, which are the great and natural highways of the jungle along and through which flows a steady and constant traffic of insect life: thus the area drained by any of these great rivers often coincides with the distributional area of a definite fauna. It is owing to this fact, together with the way in which the Senegal, Niger and Congo interlock and also on account of the comparative absence of great and high mountain barriers, that the majority of the West African Odonata are distributed evenly over so wide an area. A close parallel to this distribution is that of the Amazonian Odonate fauna.

Réne Martin's paper on the dragonflies of Grand Bassam is the only one which has been so far confined to the Odonata of the littoral of the Ivory Coast, but a number of species have been reported from this area from time to time in papers devoted to the West African fauna generally. I have been able to gather from literature a list of 26 species as coming from this area: I am now able to add to these a further 27, making a total of 53 in all. I have compared this number with that from a similar area on the West Coast of India and find that the numbers are approximately equal: thus I am of opinion that the number of 53 is not likely to be greatly exceeded in the future.

In the following list, those species marked with a dagger have been reported before, whilst those starred were included in Dr. Paulian's collection:—

LIST OF SPECIES FROM THE IVORY COAST.

Suborder ZYGOPTERA.

Superfamily AGRIOIDEA.

- † 1. *Umma cincta* (Selys).
- †* 2. *Sapho ciliata* (Fabricius).
- * 3. *Chlorocypha dispar* (Palisot de Beauvois).
- † 4. *Chlorocypha cyanifrons* (Selys).

Superfamily COENAGRIOIDEA.

- * 5. *Isomecocypha subnodalis* (Selys).
- * 6. *Elatoneura mutata* (Selys).
- * 7. *Agriocnemis macleodii* Selys.
- * 8. *Agriocnemis ebneri* Ris.
- † 9. *Agriocnemis exilis* Selys.
- †* 10. *Ceriagrion glabrum* (Burmeister).
- * 11. *Ceriagrion rubelloccinum* sp. n.
- † 12. *Pseudagrion basicornu* Martin.
- † 13. *Pseudagrion nubicum* Selys.
- * 14. *Pseudagrion angolense* Selys.
- * 15. *Pseudagrion angelicum* sp. n.
- * 16. *Pseudagrion conspicuum* sp. n.
- † 17. *Enallagma nigridorsum* Selys.

Suborder ANISOPTERA.

Family GOMPHIDAE.

- * 18. *Neurogomphus fuscifrons* Karsch.
- * 19. *Paragomphus atratus* (Selys).
- † 20. *Phyllogomphus aethiops* Selys.

Family AESHNIDAE.

- * 21. *Gynacantha sextans* McLachlan.
- † 22. *Gynacantha bullata* Karsch.

Family CORDULIDAE.

- †* 23. *Neophya rutherfordi* Selys.
- †* 24. *Phyllomacromia biflava* Martin.
- †* 25. *Phyllomacromia aequatorialis* Martin.
- † 26. *Phyllomacromia melania* (Selys).

Family LIBELLULIDAE.

- †27. *Eothemis zygoptera* Ris.
- *28. *Allorhizucha klingi* Karsch.
- †29. *Micromacromia camerunica* Karsch.
- *30. *Lokia circe* (Ris).
- *31. *Hadrothemis versuta* Karsch.
- *32. *Hadrothemis camarensis* Karsch.
- *33. *Orthetrum africanum* (Selys).
- *34. *Orthetrum chrysostigma chrysostigma* (Burmeister).
- †*35. *Orthetrum guineense* Ris.
- †*36. *Orthetrum capense* Calvert.
- †37. *Orthetrum brachiale* (Beauvois).
- *38. *Orthetrum austeni* (Kirby).
- *39. *Orthetrum microstigma* Ris.
- *40. *Acisoma panorpoides ascalaphoides* Rambur.
- †*41. *Acisoma trifidum* Kirby.
- †*42. *Chalcostephia coronata flavifrons* Kirby.
- *43. *Thermochoria equivocata* Kirby.
- *44. *Trithemis risi* Longfield.
- *45. *Trithemis stictica* (Burmeister).
- *46. *Trithemis violacea* Sjöstedt.
- *47. *Crocothemis erythraea* (Brulle).
- †*48. *Palpopleura lucia lucia* (Drury).
- †*49. *Palpopleura lucia portia* (Drury).
- †50. *Palpopleura lucia graeffi* Martin.
- †*51. *Brachythemis leucosticta* (Burmeister).
- †52. *Rhyothemis notata* (Fabricius).
- *53. *Urothemis edwardsi* Selys.

NOTES ON DR. PAULIAN'S COLLECTION.

Family AGRIIDAE.

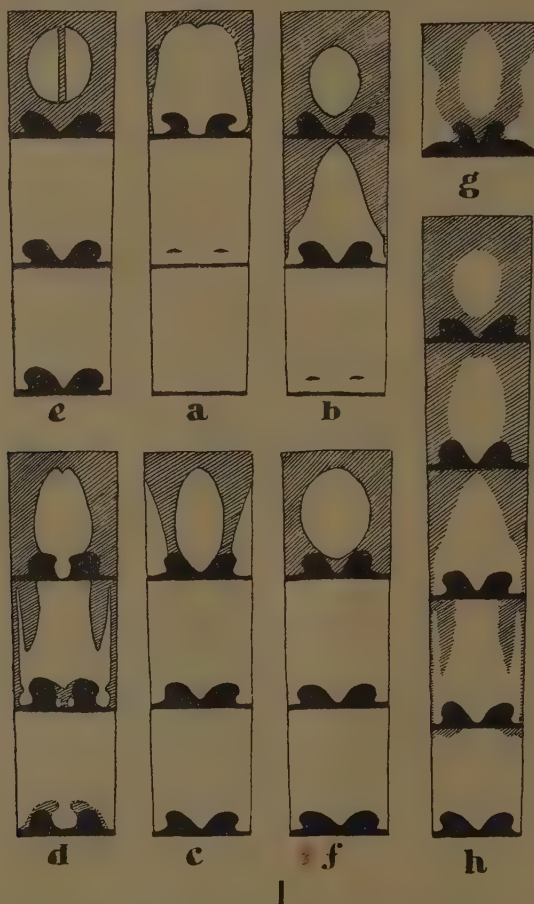
1. *Sapho ciliata* (Fabricius).

15 males, 10 females, from 3.vii to 20.vii. The majority are adult or nearly so and therefore more or less fully coloured. The most adult specimens have the wings deep coal black above and steely blue beneath, contrasting strongly with specimens in my own collection which are a beautiful metallic prussian-blue beneath. This colour may be lost in very adult age or it may have deteriorated in the present specimens. Teneral have the wings entirely hyaline or palely enfumated, iridescent but non-metallic.

2. *Chlorocypha dispar* (Palisot de Beauvois) (figs. 1 and 6c).

This species is characterised by the following complex: "1. Dorsal stripes of thorax confluent below, obsolete or interrupted above. 2. Ground-colour of abdomen blood-red throughout. 3. Segment 2 with a mid-dorsal spot of red. 4. Segment 3 broadly red on dorsum with the sides and apical borders of same irregularly black." There are 7 males and 11 females in the present collection and all, save one teneral uncoloured specimen, are almost typical but agree amongst themselves in possessing the same slight differences. In the type, in the British Museum, from Sierra Leone, the red dorsal spot on segment 2 occupies

the middle two-fourths of the segment and is oval in shape with its long axis in the same axis of the abdomen. In the present specimens, this spot is much larger, extending the whole length of the segment and bilobate in shape, one lobe occupying the basal three-fourths of the segment, the other, very much smaller and narrower, is a mere stalk connecting the larger lobe to the apical border of segment. The marking



1. Male abdominal markings of : a, *Chlorocypha selysi* Karsch, segments 2 to 4; b, *C. dispar dispar* (Beauvois), segments 2 to 4; c, *C. d. luminosa* (Karsch), segments 2 to 4, subtypical race from Uganda; d, *C. dispar pyriformosa* (Beauvois) from the Ivory Coast, segments 2 to 4; e, *C. dispar* (Beauvois), race or var. in British Museum collection, segments 2 to 4; f, *C. dispar cordosa* from Gaboon, McLachlan collection in British Museum, segments 2 to 4; g, *C. d. luminosa* (Karsch), segment 2, typical form; h, segments 2 to 6 of a hypothetical form to demonstrate the trend of evolution. (Pale areas are blood-red, cross-shading black. The black paired apical spots develop from the apical linear ones seen in figures a and b and are largely concealed later by the tertiary black markings which develop on segments 2 and 3).

on segment 3 is very similar to that of the type : segments 4 and 5 have a pair of black apical spots confluent to the apical black ring, whilst segment 6 has a vestige of this marking. These black apical or subapical spots are basic for all the markings which arise afterwards on the segments and they can be traced as present whatever the nature of the marking may be, save where the segment is entirely black. I have demonstrated this in figure 1, where the cross-shading shows the actual extent of the black markings, whilst the black portions show their basic origins, these, of course, not being differentiated in the actual specimens. It is important to keep this fact in mind, because not only are the markings present in *dispar* but throughout the Ethiopian representatives of the genus, vestigial in some, highly developed and largely concealed in others. In the type of *dispar*, these spots on segments 4 and 5 are vestigial and represented by mere elongated subapical spots. The present specimens are best regarded as racial in character, differing from type only by various modifications of the markings on segments 2 to 6, but confined to a definite area. In the McLachlan collection, a male from Old Calabar is closely similar to these Ivory Coast specimens in possessing a red oval dorsal spot on segment 2, but it is unilobate and regularly oval in shape (fig. 1, *f*) : another male in the same collection, from the Gaboon district, has a similar but more cordate shaped spot on segment 2, whilst segments 3 and 4 have paired apical spots confluent with a black apical ring. Thus this specimen resembles *luminosa* Karsch save that the mid-dorsal spot is broader and the sides of the dorsum are entirely black (red in *luminosa*). A third specimen also in the British Museum collection is similar to type except that the mid-dorsal spot on segment 2 is divided longitudinally by a black line into two small lunules (fig. 1*e*) : this marking is so unorthodox that it may possibly be an artifact. The present specimens may be named race *pyriformosa* ssp. n. ; the Old Calabar form *ovulosa* ssp. n., the Gaboon forms *cordosa* ssp. n., and Karsch's species becomes ssp. *luminosa*.

Family COENAGRIIDAE.

3. *Isomecocnemis subnodalis* (Selys) (Text-figs. 2*a* and *b* ; 8*b*).

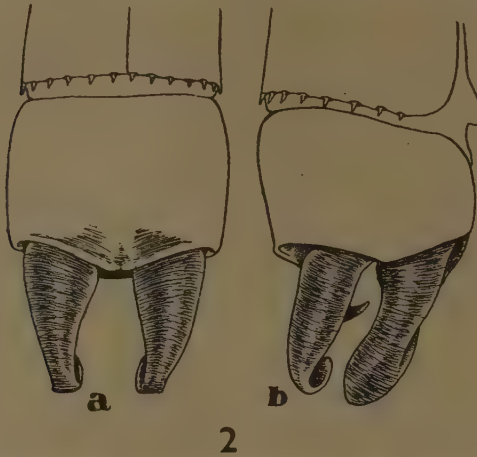
Disparoneura subnodalis Selys, 1886, *Mem. Cour. Acad. R. Belg.* 38 : 162.

Disparoneura subnodalis Selys, Kirby, 1890, *Cat. Odonata* : 133.

Disparoneura subnodalis Selys, Karsch, 1893, *Berl. ent. Z.* 38 : 36.

Isomecocnemis subnodalis (Selys,) Cowley, 1936, *Ann. Mag. nat. Hist.* (10) 17 : 515, 526, fig. 4.

There are 10 males and 6 females collected from 10.vii to 19.viii. The males have the wings deeply tinted chlorine-green ; the anal vein in all specimens ends on the cross-vein descending from the apical end of the discoidal cell, and in one specimen the anal vein lies so closely apposed to the posterior border of the wing throughout its length as to appear almost fused to it. The flexor surfaces of the femora and tibiae are conspicuously pale Cambridge blue and it is evident that the males employ this as a "recognition mark" in the same way as do many species of the CHLOROCYPHIDAE. The prothorax of the female (text-fig. 8*b*) is remarkably specialised, and Selys' description is quite inadequate ; the anterior lobe is cleft deeply into two smaller lobes each deeply hollowed out



2. Anal appendages of *Isomecocnemis subnodalis* (Selys), male, a, dorsal aspect ; b, right lateral aspect.

internally ; two slim digitate processes spring from the base of the middle lobe on its dorsum and slope so strongly forwards as almost to lie in contact with the two large mamillated processes which make up its dorsal surface. The posterior lobe is prolonged and very deeply cleft at its middle into two long thin spatulate processes which stand erect but with a slight backward inclination at the apices.

4. *Elatoneura mutata* (Selys).

1 subadult and 1 adult male, 1 very adult female, 14.vii, 20.vii, and 20.viii. An uncommon species in collections, but probably more common than it would appear to be on account of its inconspicuous coloration and the usual retiring habits of the genus. The anal appendages of the males agree very closely with Ris' good figure in the *Ann. S. Afr. Mus.* 18 : 294, f. 21.

5. *Agriocnemis maclachlani* Selys.

2 males and 1 female, 1 to 8.viii. A widely distributed species throughout tropical east and west Africa. The male is characterised among other points by the black pterostigma of the hind-wing, whereas that of the fore-wing is pale, a reversal of the usual colouring met with in the group. One of the males has the abdomen gripped by the jaws of an ant, but the body of the latter is missing, so it is impossible to determine the species.

6. *Agriocnemis ebneri* Ris.

Male.—Abdomen 16 mm. Hind-wing 10 mm.

Head: labium white, labrum and postclypeus a beautiful brilliant metallic violet ; anteclypeus, genae, bases of mandibles and beneath head pale green, rest of head above bronzed black with a pair of very small pale green round postocular spots situated very close to margin of eyes. Prothorax black on dorsum, the sides pale green, posterior lobe trilobate, the lateral lobes finely bordered with pale yellow. Thorax steely black on dorsum

to as far lateral as the antero-lateral suture, marked by complete narrow pale greenish antehumeral stripes. Laterally pale green, paling beneath thorax which is thinly pruinosed : small black spots at the upper ends of each lateral suture, that on the anterior confluent with the dorsal black in front. Legs pale green to creamy yellow with a poorly defined black stripe on outer sides of all tibiae but a well-defined black stripe on the extensor surface of hind femora, the spines and distal segment of tarsi black. Wings hyaline, 5 to 6 postnodals in fore-wing, 5 in the hind-wing, arculus very far distal to the distal antenodal, nearly as widely so as the length of the discoidal cell. Pterostigma pale yellow or bluish framed in black nervures, very long and narrow, at least four times as long as broad, outer border very oblique, the inner normally so. Abdomen green at base laterally and beneath changing to creamy yellow, then ochreous and finally ferruginous on the terminal segments. Black on dorsum from segment 1 to 7, each segment with the usual apical black ring, preapical dilatation followed by an apical constriction : segments 8 to 10 and anal appendages ochreous, probably darkening to ferruginous in full aduldage. Anal appendages very small, barely half the length of segment 10 : superiors seen in profile triangular in outline with a deep apical recess, below which is a small black spine : subtriangular as seen from the dorsum, the black spine forming the apex, the whole dorsum coated with whitish curling hairs. Inferiors slightly shorter but very broad, foliate, appearing to be two laminae folded together, the inner with a fissure on its free margin.

Habitat : The type male, along with 3 females, came from the Soudan and are the only specimens known up to the present captures. The description was made from a teneral male with incomplete colouring so that a redescription is necessary ; the descriptions of the females given by Ris, one from the adult stage, the other from an orange coloured teneral example, are good and need no repetition. A single pair from the Ivory Coast, 6.vii and 9.vii, the male almost fully adult, the female fully so, and both with the colours fully developed. The anal appendages of the male are very complicated and very small : I have not been able to improve on the figures given by Ris in 1924, *Denkschr. Akad. Wiss Wien* 99 : 277, f. 3.

7. *Pseudagrion angolense* Selys.

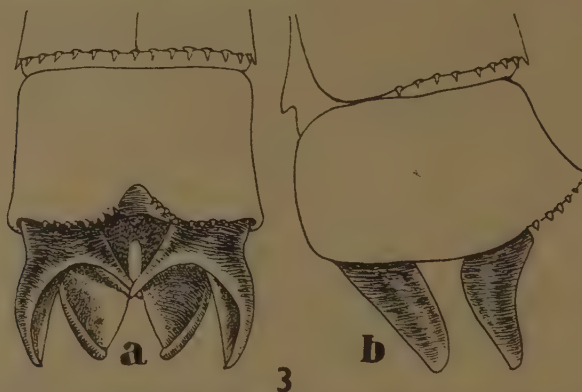
There are 2 very adult males of this moderately common and widely distributed species, 22 vii : it has been recorded from both the east and west coasts of Africa within tropical limits. The present examples belong to the old melanotic and partially pruinosed forms in which the markings are largely obscured.

8. *Pseudagrion angelicum* sp. n. (text-fig. 3).

Male.—Abdomen 30 mm. Hind-wing 18 mm.

Head : labium straw yellow ; labrum, genae and frons to as far as the bases of antennae, including the pedicel of same bright chrome yellow or tangerine orange ; rest of upper surface of head coal-black marked on occiput by a pair of very large olive green postocular spots between which run the vestiges of a yellow stripe, present as a few points only. (The postocular spots would probably change to bright chrome yellow or orange in adult males.) Prothorax black marked with chrome yellow as follows : a narrow anterior collar, a cuneiform spot on the posterior two-thirds of the dorsum of middle lobe, the two merely separated by a fine black mid-dorsal suture, a small round subdorsal spot on each side of middle lobe, two small triangular spots at middle of posterior lobe and finally the outer ends of this same lobe. Thorax black on dorsum, pale green, greenish blue or pale blue laterally, marked with bright chrome yellow antehumeral stripes, broad below, rather abruptly constricted above where the dorsal black invades the yellow locally. At this same level but to the

outer side of the humeral suture is a fine streak of yellow limited to the upper third of the shoulders. Laterally a fine black line maps out the upper part of the antero-lateral suture and expands lanceolately about midway down this suture: finally a small black spot at the upper part of the postero-lateral suture and a narrow lining of same to the inferior border of metepimeron. Beneath thorax pale, pruinosed white. Legs yellowish to ferruginous with the spines and a broad stripe along the outer side of femora black. Wings hyaline, 12 postnodals in fore-wing, 10 in the hind-wing: pterostigma very oblique, acute at both ends, olivaceous with darker centre and black framing veins: that of hind-wing one-third longer than broad, covering one cell: *ab* meeting the posterior border of wing



3. Anal appendages of *Pseudagrion angelicum* sp. n., male. *a*, Dorsal aspect; *b*, left lateral aspect.

well proximal to level of *Ac*. Abdomen bluish green at base laterally and beneath, marked with black on dorsum as follows: a quadrate spot extending from base to apical border of segment 1, a vase-shaped stripe on dorsum of segment 2 confluent apically with a narrow black ring and with a longitudinally rectangular spot of azure blue on its basal half, segments 3 to 6 with the conventional dorsal black stripes and apical rings, segment 7 similar but the stripe expanding at apical end to cover the entire dorsum and sides of segment, 8 and 9 azure blue on dorsum with narrow black apical rings covering from one-fifth to one-fourth of segment 8 and the apical third of segment 9: segment 10 entirely black as well as the anal appendages. Superior appendages about two-thirds the length of segment 10, triangular and tapering sinuously to a sharp point as seen in profile, deeply divided into two branches as seen from the dorsum, the outer branch convex outwardly, tapering to a fine point, not notched at apex, excavate within: inner branch a long robust spine directed obliquely inwards and backwards to meet and cross the apex of a similar spine from the opposite appendage. Inferior appendages of about the same length, sloping obliquely upwards as seen from the side, subconical, tapering but slightly to apex which is obtuse.

Female.—Abdomen 27 mm. Hind-wing 19 mm.

Head: labium pale brownish, almost white; labrum, clypeus, genae and frons ferruginous up to the level of lateral ocelli where a broad black band traverses the vertex broadening outwardly towards each eye, each of which is bordered narrowly with black. Posteriorly the band extends over the occiput to enclose large triangular orange or ferruginous post-ocular spots and a broken occipital stripe represented by two or three elongate small yellow spots. Prothorax ochreous marked with black but the latter colour much reduced so that the whole of the sides, most of the dorsum and the whole of the posterior lobe are pale, including the two small digitate sexual processes peculiar to this genus. Thorax golden-

green with similar black markings to the male but greatly reduced in character, thus the mid-dorsal carina is but finely black, the humeral black is incomplete and broadly interrupted below, where its continuation borders the outer side of the humeral suture. The lateral markings similarly reduced, only a small black point or elongate spot on the antero-lateral suture, which latter, above, is indicated only by the finest black line, the spot on the upper part of the postero-lateral suture vestigial. Legs as in male. Wings hyaline, 11 postnodals to fore-wing, 9 in the hind-wing: pterostigma paler, yellowish, of similar shape in all wings to that of the hind-wing of the male. Abdomen yellowish inclining to bluish green laterally and beneath especially on the basal segments, marked with black as follows: segment 1 as in the male, segment 2 with fine basal and apical black rings connected along the mid-dorsal line by an equally fine black line which expands subapically into a transverse oval dorsal spot, segments 3 to 7 similar to the male, segment 8 black on dorsum, yellowish laterally, 9 azure blue on dorsum but with a black basal ring which is confluent with a narrow mid-dorsal black stripe, segment 10 azure blue. Anal appendages black, very shortly conical.

Habitat: W. AFRICA; Ivory Coast, 2♂, 1♀. Type in Paris Museum.

This new species appears by the shape of its appendages to be nearly related to *P. basicornu* Martin, but in this latter the apex of the superior appendage as viewed in profile is distinctly notched, whereas it tapers to an acute point in *angelicum*. The colour and markings are entirely different, the latter, on the thorax of *basicornu*, being quite as much restricted as they are in the female of *angelicum*. The colour and markings are remarkably similar to those of *P. massaicum* Sjöstedt and *angolense* Selys, but the shape of the anal appendages is very different.

9. *Pseudagrion conspieuum* sp. n. (text-fig. 4).

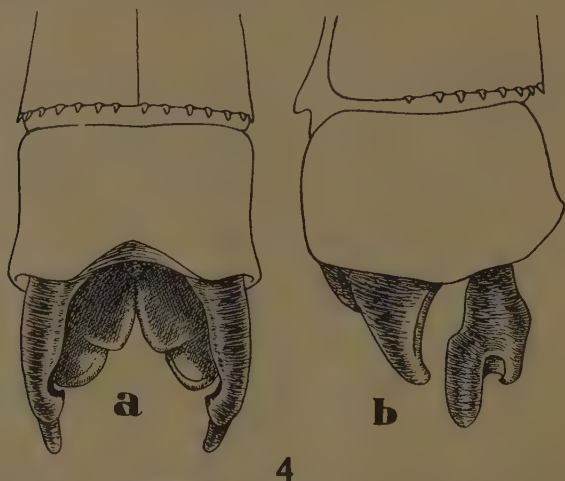
Male.—Abdomen 32 mm. Hind-wing 20 mm. Female unknown.

Head: labium straw yellow, labrum black rather broadly bordered with yellow, genae and anteclypeus pale yellow, postclypeus and frons black but the latter with a transverse rectangular chrome-yellow spot slightly notched at its middle anteriorly and sending a narrow prolongation outwards on each side to the base of antennae, the base and pedicel of which are also yellow. Rest of head black with large subrotund postocular spots of bright chrome yellow. Beneath head pale creamy yellow. Prothorax black, the anterior lobe a small subdorsal triangular spot on each side, as well as the lower parts on the middle lobe, and the outer ends of the posterior lobe all bright chrome-yellow. Thorax black on dorsum marked with chrome-yellow exactly as in the last described species (*angelicum*), the sides azure blue with a linear marking on the antero-lateral suture ending at the middle height of sides in a small black oval spot: finally a narrow and complete black stripe on the postero-lateral suture. Legs yellow with a trace of a black stripe on the distal ends of the outer sides of all femora. Wings hyaline, 13 postnodals in fore-wing, 11 in the hind-wing: *Ab* ending on the posterior border of wing distinctly distal to the level of *Ac*: pterostigma short, quadrate, rather oblique, olivaceous in colour, covering about three-quarters of a cell. Abdomen blue marked with black as follows: segment 1 with the whole of dorsum, segment 2 with a bilobate broad dorsal spot, the basal lobe about twice the length of the apical one which tapers apically to become confluent with a narrow apical black ring, the basal lobe enclosing a longitudinal oval spot of azure blue, segments 3 to 6 with the conventional black stripes and apical rings as in *angelicum*, segment 7 with the black broadening apically to cover the entire dorsum and sides, 8 azure blue, its sides black, this colour extending obliquely on to dorsum until it becomes confluent at apical border of segment with the black from the opposite side, segment 9 similar but the black still more extensive and leaving rather less than the basal half of segment blue, segment 10 black. Anal appendages black, resembling in shape those of *P. inconspicuum* Ris: the lower branch of

the superior appendages is, however, longer and pointed at its apex and the notch between the two branches very obtusely splayed: the inferior appendages are digitate in profile view and abruptly broadened at base.

Habitat: W. AFRICA; Ivory Coast, R. Banco. Type in Paris Museum.

This new species lies closest to *P. inconspicuum* Ris, from which, apart from differences in the shape of the anal appendages, it can be at once distinguished by the long petiolation of the wings and the quadrate pterostigma. The abdomen is exceedingly slender, reminding one of an *Aciagrion*. The origin of *Ab* is unique amongst the Pseudagrions, arising in all Oriental species at the exact level of *Ac* and in nearly all Ethiopian species proximal to that level: I know of no species resembling *conspicuum*, in which it arises distal to *Ac*.



4. Anal appendages of *Pseudagrion conspicuum* sp. n., male. a, Dorsal aspect; b, left lateral aspect.

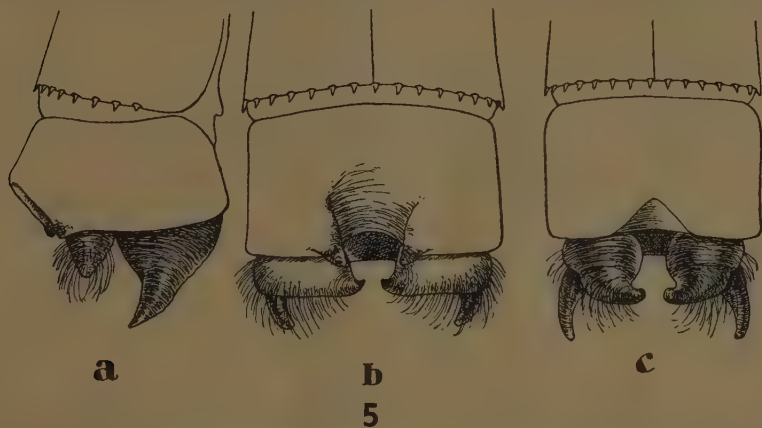
10. *Ceriagrion rubelloцерinum* sp. n. (text-fig. 5a and b).

Male.—Abdomen 38 mm. Hind-wing 22.5 mm. Pterostigma 1.25 mm.

(*Teneral condition*) Head: labium cinerous, labrum and rest of head uniform dull brown with a mere indication of rust-red developing at the site of the postocular spots: beneath head palest olivaceous. Prothorax brown, posterior lobe small, evenly rounded; thorax brown on dorsum, cinerous inclining to pale blue on the sides posterior to the humeral suture, with small oval black spots at the upper parts of the humeral and postero-lateral sutures. Beneath thorax whitish with a small black diffuse spot on each side of pectus posteriorly. Wings hyaline, uncoloured, 13–14 postnodals in fore-wings, 11–12 in the hind-wings; *Ab* prolonged proximal to *Ac* for a distance equal to the length of the latter in the fore-wing and for half that distance in the hind-wing. Pterostigma rather oblique, rectangular, only about one-quarter longer than broad, the costal side slightly shorter than the posterior, covering one cell, thus irregularly subquadrate: framed in thick black nervures which are themselves lined inwardly by clear yellow enclosing a greyish brown centre. Arculus slightly distal to the distal antenodal in all wings. Legs pale brown, knees and spines darker. Abdomen pale brown laterally, much darker on the dorsum, segment 1 with

its sides bluish, and with a black dorsal spot, segment 2 suffused with brick-red dorsally, this colour spreading on to the base of segment 3, the latter segment and 4 to 6 becoming black towards the distal ends to form conspicuous black rings; pale creamy white rings at the base of these same segments as well as subapical whitish rings basal to and bordering on the apical black rings: segment 7 similar at the base but the apical half of segment becoming brick-red: segments 8 to 10 in course of becoming red. Anal appendages pale, tipped with black.

(*Adult condition*) Differs from the teneral male by extreme melanism and by the thorax becoming white with pruinescence. Venation similar to the teneral example save that there are only 12 postnodals in the fore-wings and 10 in the hind. Head: labrum, bases of mandibles and genae turquoise blue, postocular spots a dull dark rust-red, rest of head dull black. Prothorax and thorax dull black on dorsum, clothed with dense white pruinescence on the sides and beneath, the black spots still, however, visible at the upper parts of the sutures. Legs reddish brown, knees and spines darker. Wings uniformly and palely clouded with brown: pterostigma black. Abdomen black on dorsum from segment 1 to the basal third of segment 7, the remainder bright rust-red. Sides of segments 3 to 6 with a diffuse ochreous stripe along the apical half. Anal appendages reddish tipped with black: superiors very short, less than one-third the length of segment 10: seen from above broad and flattened,



5. Anal appendages of *Ceriagrion rubelloцерinum* sp. n., male. *a*, Right lateral aspect; *b*, dorsal aspect; *c*, the same of *Ceriagrion platystigma* Fraser.

rectangular with the postero-internal corner ending in a small black spine: seen in profile this appendage is triangular and has its apex crowned with thick curling hairs. Inferior appendages robust, very broad and conical at base, tapering rapidly to a short robust spine which is directed upwards and obliquely inwards. Segment 10 viewed from behind is deeply excavate, its apical border forming a horse-shoe shaped ridge, the ends of which are thickened and terminate in blackish robust spines.

Female.—Abdomen 87 mm. Hind-wing 23.5 mm.

(*Teneral condition*) Closely similar to the teneral male, but the labium darker, the frons and vertex of head distinctly tinted with rust-red and the postocular spots definitely of this colour. A dark sooty-black area anterior to these spots runs obliquely outwards and forwards to the bases of antennae where its margin is sharply defined. Prothorax golden-brown with darker mid-dorsal line. Thorax golden-olivaceous on dorsum changing first to green and then pale blue laterally: thinly pruinose beneath and with the same small black spots on the sides as in the male. Legs as in male. Wings

hyaline, uncoloured : pterostigma similar to the male in the fore-wing but distinctly longer in the hind-wing where it is half as long again as broad ; 14 postnodals in fore-wings, 12 in the hind-wings. Abdomen similar to the teneral male but the markings more strongly contrasted and segment 2 with similar basal and apical white and black rings which completely encircle the segments ; segments 8 to 10 rust-red, segments 8 and 9 with a diffuse linear black stripe on the lower part of sides, whilst 8 has two small triangular subdorsal black spots extending along half the segment. Vulvar scale robust, reddish brown, extending slightly beyond end of abdomen.

(*Adult condition*) The specimen is slightly smaller than the teneral one, with abdomen 33-34 mm. and hind-wing 22 mm. All wings are palely enfumed with brown as in the adult male. Head as in adult male but labium blackish brown : pruinescence on prothorax and thorax confined to the lower parts of sides and beneath and bases of legs. The sides of thorax olivaceous green above, azure blue below. Legs dull reddish ochreous with black spines (4 to 5 spines on hind femora, spaced equal to their length). Abdomen entirely black on dorsum from base to apex, the only trace of paler colouring, on the sides of segments 3 to 6, which are obscurely reddish ochreous. Anal appendages and vulvar scale black, the former shortly conical.

Habitat : W. AFRICA ; Ivory Coast, one adult pair and one teneral pair, 15-19.viii.

The colouring of this new species is almost a replica of *C. cerino-rubellum* (Brulle) of the Oriental fauna and I actually mistook it at first for that species and only closer inspection showed it to be a most remarkable case of similarity through convergence. The new species is differentiated by the differently shaped pterostigma and anal appendages. The shape of the pterostigma is similar to that of *C. platystigma* Fraser, from Uganda, but the colouring of the insect and shape of anal appendages is quite different. As the figure I gave of this species in *Proc. R. ent. Soc. Lond.* (B) 10 : 63 is not quite clear, I here show an improved figure for the sake of comparison with the new species (fig. 5c). *Type* and allotype in the Paris Museum, paratypes in my own collection.

11. *Ceriagrion glabrum* (Burmeister).

A single male of this common and widely distributed African species, 10.vii, borders of the Lagoon du Banco.

Family GOMPHIDAE.

Neurogomphus fuscifrons Karsch.

Neurogomphus fuscifrons Karsch, 1890, *Ent. Nachr.* 18 : 380.

Neurogomphus fuscifrons Karsch, 1891, *Ent. Nachr.* 17 : 72.

Neurogomphus fuscifrons Karsch, Selys, 1892, *Ann. Soc. ent. Belg.* 36 : 16 (sep.).

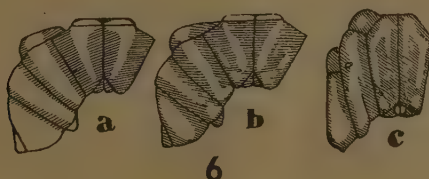
Neurogomphus fuscifrons Karsch, 1899, *Ent. Nachr.* 25 : 171.

Neurogomphus fuscifrons Karsch, le Roi, 1915, *Zentr. Afr. Exp. Zool.* : 345.

There is a single female of this rare species in the present collection : only a single male and 2 females were known hitherto, so that this third female is described rather fully here, especially as it has the colours and markings preserved almost as in life. In respect to these latter, the original description is rather poor and probably the type was in poor condition.

Female.—Abdomen 48 mm. Hind-wing 42 mm. Pterostigma 4–5 mm.

Head relatively small, transversely wide as in *Merogomphus*: labium and genae yellowish, labrum dark brown, paler along anterior border, rest of face and head glossy black. Thorax and prothorax matt black marked with citron yellow as follows: a large spot on each side of prothorax, a complete mesothoracic collar, narrow straight ante-humeral stripes confluent with the mesothoracic collar at its outer ends, thus forming inverted figures of “7.” Laterally entirely citron yellow traversed on the two sutures by narrow complete black stripes. Legs rather long, entirely black: hind femora extending to apical end of segment 1, with 5 or 6 rather short but robust spines on the distal half, and closely-set short spines on the basal half: mid-femora similarly armed but the distal spine longer. Abdomen slightly longer than the wings, rather tumid at base, cylindrical and parallel sided from apex of segment 2 to segment 6, segment 7 slightly broadened at distal end, segment 8 continuing this broadening, 9 narrowing again to 10 which is very narrow, cylindrical and with its apical half abruptly narrowed, the whole segment as long as segment 9. Anal appendages shortly conical, less than half the length of segment 10. Segment 1 yellow laterally, segment 2 with a mid-dorsal stripe extending whole length of segment, and a broad complete lateral stripe, segments 3 to 6 with narrow similar stripes but interrupted near the base on segments 4 to 6, the basal part triangular, the apical portions lessening in length from segment to segment, segment 7 with only a basolateral vestige, 8 with a broad basal ring expanding apically on mid-dorsum and again on each



6. Thoracic markings of: a, *Neurogomphus fuscifrons* Karsch; b, *Paragomphus atratus* (Selys); c, *Chlorocypha dispar* (Beauvois), male.

side so that its apical border is crenate or serrate. Segments 9 and 10 entirely black. Wings hyaline, venation black, some basal yellow tinting which extends also along the costal border: pterostigma elongate, longer in the hind-wing, narrow, strongly braced, dark ochreous or reddish brown between thick black veins: costa black. Arculus at the 2nd antenodal vein, the primary antenodals, the 6th or 7th, nodus in fore-wing slightly proximal to mid point of wing, discoidal cell of fore-wing with costal and basal sides equal, the distal side slightly longer: discoidal cell in hind-wing with costal and distal sides slightly subequal, the basal about half the length of distal: a basal incomplete subcostal vein in both fore-wings (2 in one fore-wing) and in one hind-wing: anal-loop absent: 2 rows of cells in anal field of fore-wing, 3 rows in the hind-wing: all triangles entire: *Rs* forked symmetrically: only 2 cross-veins between the sectors of arculus in fore-wing, only 1 in the hind-

wing: nodal index $\frac{16-20}{14-15} \mid \frac{19-15}{15-15}$. Vulvar scale vestigial, a mere trace of a transverse ridge, the lateral wings of the segments probably acting as substitutes.

Habitat: A single female from the Reserved Forest, Le Banco, near Abidjan, Ivory Coast, 12.vii. The type female and allotype male are in the Berlin Museum; the former differs only from the present specimen by a longer hind-wing (47 mm.).

Paragomphus atratus (Selys).*Onychogomphus atratus* Selys, 1885, *C. R. Soc. ent. Belg.* 29 : cxlvi.*Lindenis atrata* (Selys), Kirby, 1890, *Cat. Odon.* : 60.*Onychogomphus atratus* Selys, 1892, *Ann. Soc. ent. Belg.* 36 : 5 (sep.).*Onychogomphus atratus* Selys, Karsch, 1893, *Berl. ent. Z.* 38 : 31.*Onychogomphus atratus* Selys, le Roi, 1915, *Zentr. Afr. Exp. Zool.* : 344, pl. 19. f. 2, text-figs. 9, 10.

Ris, in a note in his private catalogue, expressed the opinion that this species was identical with the next species.

Onychogomphus hageni Selys.

A single pair from a stream in the Le Banco Reserved Forest are of considerable interest in that they were taken *in copula*, thus establishing the two sexes without any doubt. The female was unknown and is now described for the first time : the male differs in a few points only from the type, these differences being accounted for perhaps by different habitats. Species of this genus are characterised by the incidence of xerophilous forms in desert areas and melanotic forms in heavily forested, wet areas : the present specimens are of the latter kind.

Male.—Abdomen 33 mm. with anal appendages. Hind-wing 25 mm.

The antehumeral stripes meet the mesothoracic collar at a point only to form inverted figures of "7" : the humeral stripe is reduced to an upper triangular spot followed after a brief interval by a very short linear one, the lower half of the stripe being entirely absent. The mediolateral stripe of the thorax is also broken into an upper triangular spot and a lower linear one. Beneath thorax is dark olivaceous with the sutures and borders black. There are no basal incomplete antenodal veins present ; these are not a character of the genus and the occurrence of one such in one of the wings of the type is no doubt a pure aberration.

Female.—Abdomen 35 mm. Hind-wing 29 mm. Pterostigma 4.5 mm.

Wings hyaline, uncoloured, nodal index $\frac{12-14}{12-11} \mid \frac{15-11}{12-10}$; pterostigma black, much

longer than in the male, covering 6 cells ; 4 rows of cells in the anal field of hind-wing. The anterior border of labrum, labium and undersurface of head, the lower border of frons narrowly and a stripe across the upper surface of frons all citron yellow, rest of head and between these markings dark reddish brown. Behind occiput about 12 small spines in a right and left cluster of 6, yellow with black apices. Thorax dark reddish brown with a coppery reflex, marked with citron yellow as follows : antehumeral oblique stripes meeting the mesothoracic collar broadly to form inverted figures of "7" (much more broadly confluent than in the male), a narrow sinuous humeral stripe incomplete in its lower half and constricted but not interrupted above, 3 lateral yellow stripes, the first posthumeral with its upper end sharply angulated forwards, a narrower medial stripe interrupted as in the male, and lastly a posterior one which covers the greater part of the mesepimeron, curved strongly and with its concavity looking forwards. Beneath reddish brown. Legs : femora yellow, the anterior pair marked with black outwardly and anteriorly, all others black at distal ends and all coated on flexor surfaces with a dense field of small black spines. Tibiae and tarsi black. Abdomen black marked as in the male with the yellow markings, however, more extensive : segments 2 to 4 with broad dorsal stripes which shorten from segment to segment and occupy only the middle two-fourths of segment 4. Segment 7 with its basal half yellow, 8 and 9 with large basal spots on the sides only, segment 10 and the anal appendages entirely black. The latter as long as segment 10, very acute : vulvar scale as in *P. cognatus* (Rambur), very short and bifid.

Habitat: The type is from the Belgian Congo and is now in the Brussels Museum. Only 3 males and a single female are known. Karsch states that the occipital spines are absent in group *cognatus* of genus *Onychogomphus* (*Paragomphus*) to which this species belongs, but he is in error here as the female of *cognatus* has 6 well-developed spines behind its occiput, in two groups of 3, a right and a left; to see these it is usually necessary to remove the head and to view it under a microscope.

FAMILY AESHNIDAE.

Gynacantha sextans McLachlan.

Gynacantha sextans McLachlan was described from a male from the Cameroons: the type, in the British Museum, is the only known specimen. There is an enormously robust female *Gynacantha* in Dr. Paulian's collection from the Reserved Forest, Le Banco, 18.viii., with a note on the packet to the effect that it is always crepuscular. I gather from this that a number of specimens were seen but only one captured: its size, venation and colouring all agree closely with *sextans*, and I do not think there is any doubt about the determination. Its abdomen measures 56 mm. without the anal appendages, the latter being shorter than is usual in the genus, and finely tapered, lanceolate and shorter than segment 9. The apices are intact and not fractured off as is so often the case in the female, this damage occurring during the act of ovipositing in dry soil. The venation is close, costa reddish brown, membrane white,

primary antenodals the 8th or 9th: nodal index $\frac{20-28}{25-22} \mid \frac{28-21}{22-23}$;

discoidal cells $\frac{6}{7} \mid \frac{6}{7}$; cubital cross veins $\frac{8}{7} \mid \frac{7}{6}$; anal loop 14/14. *Rs* is forked well before the pterostigma and there are 5 to 6 rows of cells between it and *Rspl*: pterostigma covers 4 cells, is rather long and reddish ochreous in colour. The general colouring is dark reddish brown, darkest on the dorsum of thorax; the occiput yellow, and the frons bearing a thick black "T" on its upper surface. The legs are uniform bright reddish brown. Abdomen of the same colour but deepening dorsally to blackish brown; segment 8 is short and very stout, segment 9 is at least half as long again as 8 and tapers analwards, thus differing from most other species of the genus.

[Whilst writing up these notes a second female was sent to me from the Paris Museum, taken at Libongo, W. AFRICA, viii.39, by Mr. Lepesme. This specimen is somewhat smaller—abdomen 53.2 mm. and hind-wing 50.4, contrasted with abdomen 59–60 mm. for type and 56 for the Ivory Coast specimen; hind-wing 50–53 mm. for type and 53 for the Ivory

Coast one. This Libongo specimen has a nodal index of $\frac{20-26}{22-20} \mid \frac{28-22}{21-24}$:

discoidal cells $\frac{7}{6} \mid \frac{6}{6}$; cubital cross veins $\frac{7}{6} \mid \frac{7}{7}$; anal-loop 12/14, which figures agree closely with the type and with the Ivory Coast female. The wings are irregularly infuscated more especially distal to the nodus, along the posterior border of wings and at the apices. The black "T" on

the frons is well defined. The Ivory Coast female has the wings clear but is probably a younger specimen ; the type has the wings infuscated.]

Gynacantha bullata Karsch.

A single male, 12.viii, from Le Banco Forest, is entirely typical.

Family CORDULIDAE.

Phyllomacromia biflava Martin.

A single male differs only by the yellow markings which are more restricted than in the type. Border of lagoon du Banco, 10.viii.

Phyllomacromia aequatorialis Martin.

A single male with the same data as the last. Does not differ in any respects from Martin's description.

Neophya rutherfordi Selys.

Neophya rutherfordi Selys, 1881, *C. R. Soc. ent. Belg.* 25 : 17.

Neophya rutherfordi Selys, Kirby, 1890, *Cat. Odon.* : 46.

Neophya rutherfordi Selys, Martin, 1906, *Cat. Coll. Selys, Cordulines* 17 : 8.

Neophya rutherfordi Selys, Martin, 1912, *Feuill. jeun. Nat.* (5) 42 : 99.

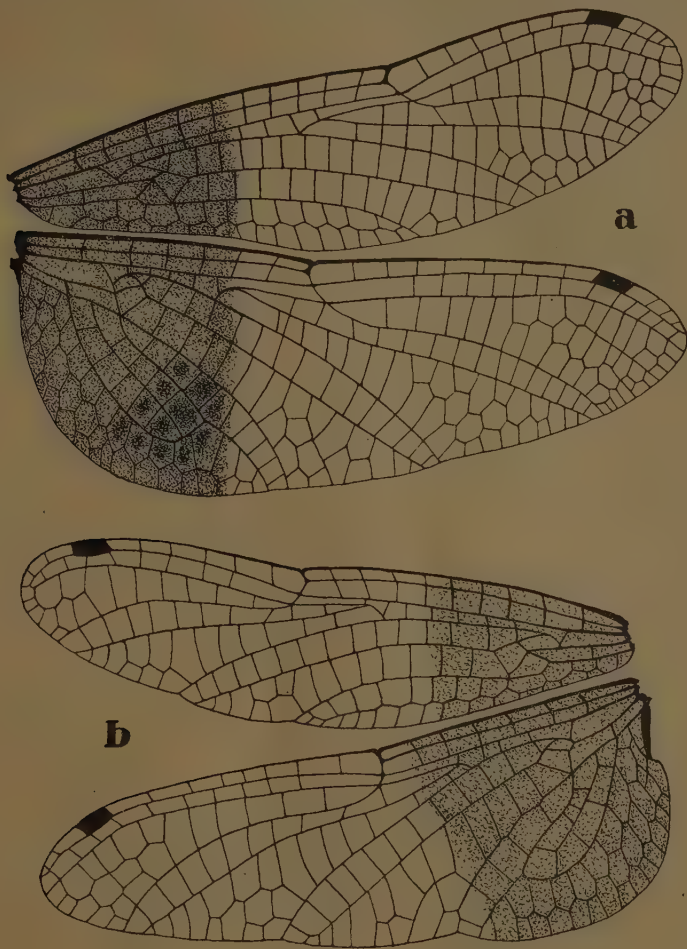
Neophya rutherfordi Selys, Morton, 1928, *Ent. mon. Mag.* 64 : 121.

Female.—Abdomen 19 mm. Hind-wing 25 mm. Pterostigma 1 mm.

Head : labium yellow, labrum steely blue black, anteclypeus pale, cinereous ; post-clypeus, frons and vesicle glossy metallic blue black ; occiput very small, steely blue black ; eyes brown but probably dark emerald green during life. Prothorax black on dorsum changing to brown laterally. Thorax metallic bluish green (prussian blue) on dorsum as far lateral as the level of the spiracle, the sides pale creamy yellow traversed by a broad stripe of metallic dark blue which is centred over the postero-lateral suture and continued under the ventrum to become confluent with the stripe from the other side. A moderately broad creamy yellow stripe in the humeral region and occupying the lower two-thirds of the dorsum only. Legs blackish brown, coxae, trochanters and distal three-fourths of the two hind pairs of tibiae pale yellow : some fine hairs on the femora and very long, rather closely-set hair-like spines on the tibiae, decreasing rapidly in length distally. Claw-hooks long, equal to the ends of claws which thus appear to be bifid. Wings hyaline, palely and evenly enfumed throughout but deepening somewhat towards the apices and the cell middles paler, giving a mottled appearance to the wings : the bases of both pairs broadly tinted with deep amber yellow to as far distal as the level of the 5th antenodal vein in both wings and with an outer border which runs straight back to the posterior border of wings. In full adults a dark infuscated irregular spot is present in the hind-wings occupying the centres of about 12 cells and centred over the apex of the anal-loop. This spot entirely absent in the teneral condition and occupying only the 3 terminal cells of the anal-loop in sub-adults. Venation closely similar to that of male and as shown in figure (fig. 7). Abdomen steely black marked with pale creamy yellow as follows : segment 2 with a large rounded subdorsal spot on each side, its ventral side pale and almost white, this colour being continued basad and dorsad and ending squarely on the sides. Segments 3 to 7 with broad lateral stripes, traversing the whole length of segment 3, three-fourths of segment 4, as far as the jugal suture on 5 and 6 and rather short of this level on 7. Rest of abdomen unmarked. Anal appendages very shortly conical. Vulvar scale short, buckled triangularly inwards at its apex, which is followed by a thin transverse ridge at the outer ends of which are short thin digitate processes.

Habitat : Two males and two females taken in forest clearings west of Abidjan, Ivory Coast. The male type now in the British Museum (Natural History) came from Old Calabar. I possess a second male from Sierra Leone, so that the species is distributed from the Gold Coast to

the Gaboon. The rediscovery of this interesting insect has permitted me to make a fuller description and to correct the former ones. The figure of the male wings given by Martin in the *Cat. Coll. Selys, Cordulines*, fig. 6, shows the base of the hind-wing too greatly expanded and



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7. Wings of *Neophya rutherfordi* McLachlan : a, female ; b, male.

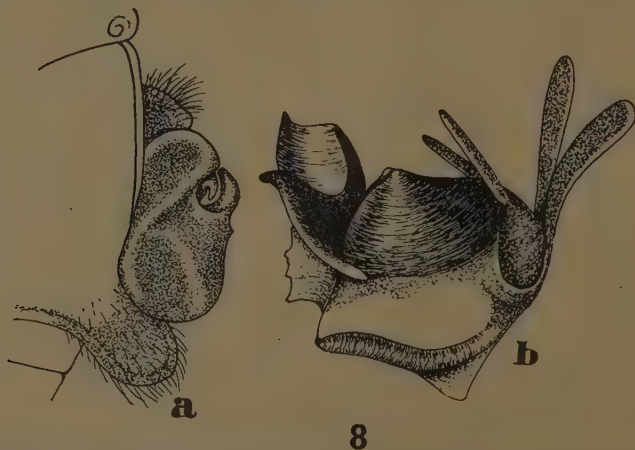
has not brought out the characteristic crenated hind borders of the wings : thus I have taken this opportunity to refigure the wings of both sexes (text-figure 7a and b). The position of the genus *Neophya* in the family CORDULIIDAE is not clear : in the "Reclassification of the

Odonata," Tillyard and Fraser, I included it in a new subfamily, the NEOPHYINAE, but I am inclined now to revise that view in the light of the new evidence afforded by the female. The evolution of the nodal index is as high as that attained by the most recent LIBELLULIDAE and the arcus shows an equally high recession, yet we find these modern products associated with extremely archaic elements such as accessory veins to the bridge, four-sided discoidal cells, absent *Rspl* and so on. In the face of such anachronisms I can only think that this species is a highly specialised one and that the apparently vestigial elements found are due to a secondary reduction in the venation brought about by a lessening strain thrown on the wings. *Neophya* bears a remarkable resemblance to *Idionyx* in the colouring, the poorly chitinized body and, I suspect, the habits. *Idionyx* only flies in bright sunlight and soars and floats like gossamer on the ascending currents of warm air. Even the obscuring of sunlight by a passing cloud is sufficient to drive them from the air. Thus I think that *Neophya* has come from the same ancestral line as *Idionyx* and the genus should now find a place in the subfamily IDIONYCHINAE. Dr. Paulian confirms that the flight of *N. rutherfordi* is similar to that of *Idionyx*.

Family LIBELLULIDAE.

Allorhizucha klingi Karsch (fig. 8a).

There are 19 males and 7 females of this little known dragonfly, all taken during the months of June to August but more especially during July. Whilst I am satisfied in the correct identification of these specimens, I find that the genitalia are not in strict accord with the figure 49 shown in Ris, 1909, *Cat. Coll. Selys (Libellulines)* 9: 81; the lobe is more rounded and the hamules distinctly overlap it, whilst the apices of the hamules are both visible in profile view as if interlocked. Of the 32 known examples, 27 are in the Selysian collection.



8. a, Male genitalia of *Allorhizucha klingi* Karsch; b, prothorax of *Isomecocrnemis subnodalis* (Selys), female.

Lokia circe (Ris).

A single female, 20.vii.45, is with some doubt determined as such. It agrees closely with the Risian description made from a single juvenile male and female, the only specimens known.

Hadrothemis versuta (Karsch).

Only 11 males and a single female appear to have been collected heretofore of this fine species, so that it is surprising to find no less than 16 males and 9 females in the present collection. All males are of the red form and there is but slight evidence of pruinescence on segments 3 to 5 in any of the specimens. The basal markings of wings are less extensive than in the type; up to the 1st antenodal in the fore-wings and as far as the cubital vein, but extending to the 4th antenodal and middle of discoidal cell in the hind-wings. The abdomen varies from dark blood-red to black. The description of the allotype female in the British Museum given by Ris is incomplete and the following additional notes are now given:

Frons violet metallic, thoracic markings obsolete (or may have changed from decomposition), the whole an uniform brownish yellow, abdomen dark reddish-brown with the carinae mapped out in black. Wing apices only narrowly bordered with brown: dark streaks in the fore-wings extending up to the 1st antenodal and the cubital cross vein, but up to the 3rd antenoidal and whole of cubital space in the hind-wings, where the coloured areas are very sharply (not diffusely) limited. Nodal index of female: $\frac{9-15}{11-112} \mid \frac{15-9}{12-10}$.

Hadrothemis camarensis (Kirby).

A single male, 11.viii, appears to belong to this species; it actually works out to *H. versuta* (Karsch) in the Risian key, but there are 2 rows of cells between *MA* and *Mspl* in the fore-wings, and the basal markings are so pale as to be almost obsolete. It agrees with *versuta* in possessing only a single cross-vein in the cubital space of the hind-wings. Its large size further suggests *camarensis*, of which it is perhaps an aberrant example.

Orthetrum africanum (Selys).

Four males all dated 28.vii. The species appears to be of local distribution and not at all common. The present specimens have been determined by their genitalia, which agree with figure 145 in Ris, 1c.

Orthetrum guineense Ris, and *O. capense* Calvert.

There are 2 males of *O. guineense* and 15 males and 4 females of *capense* in the present collection. Both are common species and rather widely distributed. It seems best to treat these two as species rather than subspecies of *chrysostigma* and *stemmale* respectively as was done in 1909 by Ris, who, however, did raise the status of *guineense* to specific rank in 1916 (Ris, 1916, *Cat. Coll. Selys, Libellulines*, 16 : 1082).

Orthetrum austeni (Kirby).

One adult male and one teneral female of this magnificent *Orthetrum* are found in Dr. Paulian's collection, both taken in August. The base of the hind-wings of the male is colourless: there are as many as 8 cells in the subtrigone of fore-wings (6 shown in the wing figured by Ris (*loc. cit.*, fig. 139), but 7 given in the text.) It is quite the largest species of *Orthetrum* known, even exceeding the dimensions of *angustiventre* (Rambur) and *melania* Selys.

Orthetrum microstigma Ris.

One male, 22.vii. Determined by the genitalia which agree closely with the figure given by Ris (*loc. cit.*, fig. 626).

Acisoma panorpoides ascalaphoides Rambur and
Acisoma trifidum Kirby.

Numerous specimens belonging to both sexes of these two common species are represented in the present collection, all taken during July and August.

Chalcostephia coronata flavifrons Kirby.

A single male, 24.vii. A species widely distributed throughout tropical Africa but nowhere common. I possess specimens collected by Professor G. D. Hale Carpenter in Uganda, an area not mentioned in Ris, most of whose localities are in West Africa.

Thermochoria equivocata Kirby.

One pair, 30.viii, apparently taken *in copula*. The two specimens agree with the type rather than with var. *picta* Sjöstedt.

Trithemis violacea Sjöstedt.

A single male, 21.vii, determined by its colouring and markings with considerable doubt. I am of opinion that little separates this species from *annulata* (Beauvois) from the same area. The species is known from a single male and two females in the Stockholm Museum. The differences between it and *annulata* are well summed up by Ris (*loc. cit.*, 1912, 14: 772). The colouring and markings of the red forms belonging to the genus *Trithemis* undergo remarkable changes from the teneral to the adult condition, and in some species—*e.g.*, *aurora* (Burmeister)—even the abdomen changes its shape as the insect passes from the juvenile to the adult state.

Urothemis edwardsi Selys.

There are 3 females of this fine species in the collection, all collected in the month of July. One of these is typical with the basal marking of the usual bright golden yellow with included black marking; the other two are remarkable as being andromorphs, with the basal marking of the hind-wings as in the male, a form which has not hitherto been described. Moreover, the basal marking is very extensive in the hind-

wing, where it reaches half-way between the 1st and 2nd antenodals, covers the proximal half of the discoidal cell and at that level runs straight back through the anal-loop to attain its inner border and then curves basad to reach the extreme tornal angle of the wing. Proximally it reaches the extreme basal border of the wing whilst outwards there is but the narrowest areola of golden brown. The whole area is steely black save for a fine horizontal hyaline line in the median space. In females from Uganda which I possess, the basal marking covers less than half this area although of the same dark blackish brown.

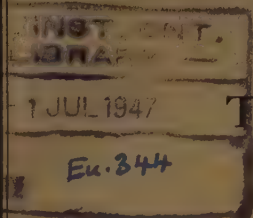
Habitat: Collected whilst ovipositing in the lagoon, 12.vii, near Abidjan, IVORY COAST.

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NEW SPECIES OF *LIPOSCELIS* MOTSCHOUJSKY (CORRODENTIA, LIPOSCELIDAE) IN ENGLAND¹

BY EDWARD BROADHEAD, M.A., B.Sc., F.R.E.S.
(Lecturer in Zoology, University College of the South-West, Exeter.)

Manuscript received 18th July, 1946.

(Read 6th November, 1946.)

WITH ONE PLATE AND 9 TEXT FIGURES.

THE following four species of *Liposcelis* have been taken from cellars or dusty shelves in England. Three of these species have also been found in granaries. It is doubtful whether any of them can survive outdoors, since they appear to be specifically distinct from the few species which are known to live in natural habitats in this country. A detailed study of a number of possibly specific characters has been made to estimate the nature and extent of the differences between these species. For this purpose, the animals were cultured at 25° C. and 76% R.H. on a diet of yeast (crushed "Aluzyme" tablets) to obtain sufficient numbers of both sexes for a statistical study. These results have been compared in one instance with a similar study of a number of wild females obtained from the Biological Field Station cellar, Slough, where the temperature was much lower than under culture conditions. The cultures of *L. liparus* and *luridus* were derived from a small number of wild caught specimens. Cultures of *L. pubescens* and *subfuscus* were each reared from a single fertilised female.

Holotype (♀) and paratype (♂) of each species are deposited in the Hope Department of Entomology, University Museum, Oxford. The paratypes are in my collection.

Brief notes on diagnostic characters for these four species and for *L. granicola* Broadhead and Hobby, 1944, are given, but a full discussion of these with reference to other described species is reserved for future publication.

I wish to express my thanks to Mr. D. A. Kempson of the Department of Zoology and Comparative Anatomy, Oxford, for taking the photomicrographs, to the British Council for permission to reproduce my drawing of *L. granicola* (fig. 2), and to the University College at Exeter for a grant covering the cost of the photomicrographs.

¹ Since this paper went to press descriptions of two *Liposcelis* species have been published by Pearman (1946, *Entomologist* 79 : 235-244). The first is a redescription of *L. divinatorius* (Müll.). Mr. Pearman has kindly allowed me to examine one of his specimens of this species. It is identical with my *luridus*. My specimens have been described here as a new species since there has been considerable confusion in the literature with regard to the identity of *divinatorius* and since my specimens appeared to differ from Hagen's description of this latter species. Hagen described *divinatorius* as bone yellow, glossy and with a greasy lustre and gives the antennal length as 0.56 mm., a considerable difference from *luridus*. Moreover Hagen probably had a mixture of species. Pearman's *L. mendax* is distinct from any of the five species described here.

Liposcelis liparus sp. n. (figs. 1, 4-9, and Pl. 1, figs. 1, 4).

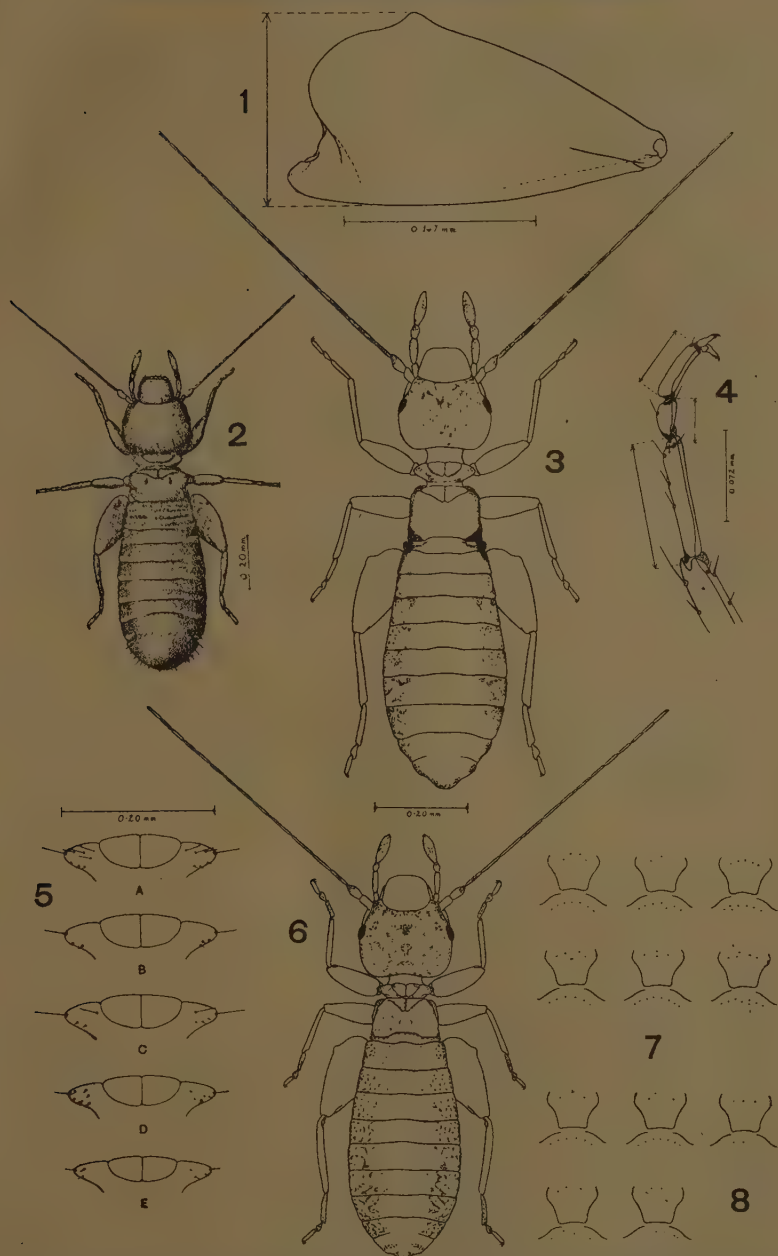
Female. Colour: Body semi-transparent. Upperside: glossy brown; cranium and prothorax Tawny-Olive, with large numbers of red pigment granules on epicranium, not arranged in a constant pattern, and on prothorax particularly in sutural depressions; clypeus more reddish; eyes black; meso-metathorax Olive-Brown, with red pigment granules sparsely scattered posteriorly and laterally, absent anteriorly and medially except in sutural depressions; antennae, maxillary palpi and legs as meso-metathorax; tarsi paler; terminal three segments of maxillary palpi, second antennal segment distally and the two proximal tarsal segments with red pigment granules; abdominal tergites 3-7 inclusive each divided into two transverse bands of equal width, the posterior band Buffy-Brown, the anterior one only slightly darker medially, much darker (Olive-Brown) laterally; tergites 8-10 inclusive, except posterior region of tergite 8 laterally (Buffy-Brown), uniformly dark brown (Mummy Brown), the contrast in colour between these and the more anterior tergites appearing more evident at lower magnifications; anterior borders of tergites 3-8 inclusive each with a very narrow transverse dark brown medial streak about half as long as width of abdomen; tergites 1 and 2 with dark red pigment granules scattered uniformly, the remaining tergites with similar pigment granules confined to a longitudinal band on each side of width equal to one-third width of abdomen. Underside: glossy brown (Tawny-Olive); mouth parts more reddish; subgenital plate laterally and posteriorly, paraprocts and epiproct dark brown (Mummy Brown); red pigment granules densely distributed on anterior and lateral margins of pro- and meso-metathoracic sternites, more diffusely at base of hind femora and very sparsely scattered on head and on abdominal sternites laterally. In some individuals the fat body is visible as small pale brown or whitish patches on abdomen, thorax and head, chiefly in frontal and occipital area. The fat body is much more conspicuous in alcohol-preserved specimens. Some newly captured individuals had very conspicuous opaque white fat bodies, resulting in a dark brown and white mottled appearance, which has not been observed in large numbers of yeast fed laboratory reared specimens.

Sculpturing (Pl. 1, figs. 1, 4): head dorsally with indistinct arched ridges enclosing smooth transverse spindle-shaped areas; abdominal tergites almost smooth but showing at high magnifications ($\times 1250$) pentagonal or hexagonal areas, enclosing darkly stained dots much smaller than the tubercles present in the other species, the areas separated by more lightly stained tracts bordered by rows of such dots. Epicranial suture very indistinctly indicated by a slight break in the sculpturing.

Head: with short fine hairs uniformly scattered, length of hairs slightly greater than width of adjacent spindle-shaped areas on cuticle, distance between hairs about three times length of hairs. Third antennal segment with 16-27 annular ridges (Table 3)—in 20 specimens, 1 with 16, 2 with 18, 2 with 19, 2 with 20, 5 with 21, 5 with 22, 2 with 25, 1 with 27 annular ridges (antennae with less than 15 segments and many more annular ridges on segment 3 not infrequent). Eye with 5-7 ommatidia (Table 3)—in 32 eyes, 5 with 5, 9 with 6, 18 with 7 ommatidia (in 4 individuals the number of ommatidia differed in right and left eyes.)

Thorax: with short fine hairs uniformly scattered as on head; with two stronger and longer bristles, truncated distally (fig. 5), on prothorax laterally on each side, one on lateral tip ("humeral seta," Table 1), the other shorter and thinner and situated anteriorly near humeral seta, and with 2-3 small fine hairs posteriorly near humeral seta. Prothoracic sternite (fig. 7, Table 4a) with 3-5 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 14 per cent. with 3 bristles, 80 per cent. with 4, 6 per cent. with 5. Meso-metathoracic sternite (fig. 7, Table 4a) with transverse slightly arched row of 6-8 bristles towards anterior margin—in 50 specimens, 2 per cent. with 6 bristles, 74 per cent. with 7, 24 per cent. with 8.

Abdomen: with short fine hairs uniformly scattered as on head; with long strong bristles, truncated distally and dilated apically, on 8th, 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; five such bristles on each side of almost equal



FIGS. 1-8.—1, *L. liparus* ♀ right hind femur posterior view showing measurement taken. 2, *L. granicola* ♀ dorsal view. 3, *L. luridus* ♂ dorsal view showing distribution of pigment granules. 4, *L. liparus* ♀ hind tarsal segments showing measurements taken. 5, ♀ prothorax dorsal view to show chaetotaxy: A, *L. pubescens*; B, *L. luridus*; C, *L. liparus*; D, *L. subfuscus*; E, *L. granicola*. 6, *L. liparus* ♂ dorsal view showing distribution of pigment granules. 7, *L. liparus* ♀ diagrams to show variation in chaetotaxy of thoracic sternites. 8, *L. liparus* ♂ diagrams to show variation in chaetotaxy of thoracic sternites.

length and longer than the adjacent bristles, one of these on lateral margin of 8th tergite, two on lateral margin of 9th and two on lateral margin of 10th tergite (fig. 9), the bristle measured (Table 1) situated more dorsally on lateral margin of 9th tergite between basal horns of gonopods. Towards base of epiproct on each side of mid-line a single extremely long fine curved hair, pointed at its extremity (Table 1). Abdominal tergites 1 and 2 slightly but uniformly sclerotized.

Body length 1.13–1.32 mm. (20 measurements). Various body measurements are given in Tables 1, 3, 4a.

ENGLAND: on dusty shelves in Hope Department of Entomology, Oxford, 17th September, 1941 (type locality); in cellar on old paper, 25th March, 1943, and in microscope slide box, 20th September, 1943, at Biological Field Station, Slough, Bucks.

Male. Colour (fig. 6): Body semi-transparent. Upperside: shiny brown; cranium, thorax and abdomen Buffy-Brown with only slight differentiation in colour between anterior and posterior regions of abdominal tergites; apex of abdomen slightly darker; clypeus more reddish; eyes black; antennae, maxillary palpi and legs as abdomen; tarsi almost colourless; red pigment granules, not arranged in a constant pattern, on head, scattered uniformly on pro- and meso-metathorax and confined on abdomen to a longitudinal band on each side of width equal to one-third width of abdomen. Underside: uniformly shiny brown (Buffy-Brown); mouth parts more reddish; red pigment granules densely distributed on anterior and lateral margins of pro- and meso-metathoracic sternites, more diffusely on head and very sparsely on abdominal sternites laterally. Unlike the females, the fat bodies of laboratory bred males are usually not evident except when preserved in alcohol.

Sculpturing: as female.

Head: with short fine hairs uniformly scattered, length of hairs slightly greater than width of adjacent spindle-shaped areas on cuticle, distance between hairs 3–4 times length of hairs. Third antennal segment with 13–17 annular ridges (Table 3)—in 20 specimens, 1 with 13, 7 with 14, 5 with 15, 6 with 16, 1 with 17 annular ridges (antennae with less than 15 segments and many more annular ridges on segment 3 not infrequent). Eye with 4–5 ommatidia (Table 3)—in 20 eyes, 1 with 4, 19 with 5 ommatidia.

Thorax: with short fine hairs uniformly scattered as on head; with one stronger and longer bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta," Table 2) and with 1–2 small fine hairs posteriorly near humeral seta. Prothoracic sternite (fig. 8, Table 4b) with 3–4 bristles anteriorly arranged in a transverse arched row—in 50 specimens 96 per cent. with 3 bristles, 4 per cent. with 4. Meso-metathoracic sternite (fig. 8, Table 4b) with transverse slightly arched row of 5–7 bristles towards anterior margin—in 50 specimens 10 per cent. with 5 bristles, 56 per cent. with 6, 34 per cent. with 7.

Abdomen: with short fine hairs uniformly scattered as on head; with long strong bristles, truncated distally and slightly dilated apically, on 8th, 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; five such bristles on each side of almost equal length and longer than the adjacent bristles, one of these on lateral margin of 8th tergite, two on lateral margin of 9th and two on lateral margin of 10th tergite, the bristle measured (Table 2) situated laterally on 8th tergite. Towards base of epiproct on each side of mid-line a single extremely long fine curved hair pointed at its extremity (Table 2). In freshly killed specimens 6th, 7th and 8th tergites with anterior and posterior transverse brown bands, the posterior band of 8th tergite divided medially by a colourless area, these not visible in stained preparations; remaining tergites uniformly sclerotized.

Body length 0.84–0.93 mm. (20 measurements). Various body measurements are given in Tables 2, 3, 4b.

***Liposcelis luridus* sp. n. (figs. 3, 5 and Pl. 1, figs. 2, 5).**

Female. Colour: Body semi-transparent. Upperside: dull buff; cranium, thorax and abdomen uniformly Warm Buff; red pigment granules scattered sparsely on head, forming no constant pattern, on lateral regions of thorax, but absent in sutural depressions, sparsely scattered or absent on abdomen; clypeus more reddish; eyes black; antennae, maxillary palpi and legs as abdomen; tarsi much paler; terminal segment of maxillary palpi and second antennal segment with red pigment granules, such granules absent on tarsi; abdominal tergites 5-7 inclusive each divided into two transverse bands, the posterior one narrower and only slightly lighter. Underside: uniformly glossy Warm Buff; mouth parts more reddish; red pigment granules distributed on margins of thoracic sternites more densely anteriorly, aggregated in a small group at base of hind femur near articulation with coxa and very sparsely scattered or almost absent on head and on abdominal sternites 1-4 laterally. In some individuals the fat body is visible as small whitish patches on head, thorax and abdomen.

Sculpturing (Pl. 1, figs. 2 and 5): Head dorsally with distinct arched ridges enclosing transverse spindle-shaped areas bearing distinct minute tubercles. Abdominal tergites with transverse spindle-shaped areas enclosing distinct tubercles, the areas separated by plain narrow tracts bordered by rows of tubercles. Epicranial suture indicated by a break in the sculpturing. An internal thickening of the cuticle is present beneath the posterior third of the epicranial suture.

Head: with short fine hairs uniformly scattered, length of hairs approximately equal to width of adjacent spindle-shaped areas on cuticle, distance between hairs as in *L. liparus*. Third antennal segment with 14-20 annular ridges (Table 3)—in 20 specimens, 1 with 14, 2 with 16, 7 with 17, 4 with 18, 2 with 19, 4 with 20 annular ridges. Eye with 7 ommatidia (Table 3)—in 25 eyes, 100 per cent. with 7 ommatidia, their arrangement constant.

Thorax: with short fine hairs uniformly scattered as on head; with one stronger and longer bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta", Table 1) and with 1-4 small fine hairs posteriorly near humeral seta (fig. 5). Prothoracic sternite (Table 4a) with 4-7 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 38 per cent. with 4 bristles, 34 per cent. with 5, 22 per cent. with 6, 6 per cent. with 7. Meso-metathoracic sternite (Table 4a) with transverse slightly arched row of 6-10 bristles towards anterior margin—in 50 specimens, 2 per cent. with 6 bristles, 48 per cent. with 7, 28 per cent. with 8, 16 per cent. with 9, 6 per cent. with 10.

Abdomen: with short fine hairs uniformly scattered as on head; with long strong bristles, truncated distally and dilated apically, on 8th, 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; five such bristles on each side of almost equal length and longer than the adjacent bristles, one of these on lateral margin of 8th tergite, two on lateral margin of 9th and two on lateral margin of 10th tergite, the bristle measured (Table 1) situated more dorsally on lateral margin of 9th tergite, between basal horns of gonopods. Towards base of epiproct on each side of mid-line a bristle (Table 1), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 9th tergite laterally. Tergites 1 and 2 (in stained preparations) each divided into two transverse bands interrupted medially, width of the three anterior bands subequal, posterior band of segment 2 of width almost twice width of each of the more anterior bands. Remaining tergites uniformly sclerotized.

Body length 1.15-1.39 mm. (20 measurements). Various body measurements are given in Tables 1, 3, 4a.

ENGLAND: in collection of insects, Batley, Yorkshire, 25th December, 1943 (type locality); on dusty shelves at Biological Field Station, Slough, Bucks, 14th September, 1943; in grain dust (N. Manitoba wheat) from walls and floor of Symon's Wharf, London, 18th May, 1944; in barley shavings from Sharpness, Glos., 19th September, 1944.

Male. Colour (fig. 3) : Body semi-transparent. Upperside : dull light buff ; cranium, thorax and abdomen uniformly Light Buff with no differentiation in colour between anterior and posterior regions of abdominal tergites ; clypeus more reddish ; eyes black ; antennae, maxillary palpi and legs as abdomen ; tarsi colourless ; terminal three segments of maxillary palpi and second antennal segment distally with red pigment granules, such granules in dense aggregates on antennal segments 3-6 inclusive ; red pigment granules distributed on head in small groups or tracts or almost absent, densely packed on prothorax laterally and posteriorly, very densely aggregated on lateral margin and postero-lateral angle of meso-metathorax and on antero-lateral region of 1st abdominal tergite and sparsely scattered in a longitudinal band on each side of remaining abdominal tergites. Underside : uniformly glossy Light Buff ; mouth parts more reddish ; red pigment granules distributed on margin of thoracic sternites particularly on antero-lateral regions, very sparsely scattered on postero-medial region of head and on abdominal sternites laterally, and aggregated in a small group at base of hind femur near articulation with coxa. Unlike the females, the fat bodies of laboratory bred males are not usually evident except when preserved in alcohol.

Sculpturing : as female.

Head : with short fine hairs uniformly scattered, as female. Third antennal segment with 13-19 annular ridges (Table 3)—in 20 specimens, 2 with 13, 4 with 14, 9 with 15, 3 with 16, 1 with 17, 1 with 19 annular ridges. Eye with 5 ommatidia (Table 3)—in 24 eyes, 100 per cent. with 5 ommatidia, their arrangement constant.

Thorax : with short fine hairs uniformly scattered as on head ; with one stronger and longer bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta," Table 2) and with one small fine hair more posteriorly near humeral seta. Prothoracic sternite (Table 4b) with 3-5 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 74 per cent. with 3 bristles, 22 per cent. with 4, 4 per cent. with 5. Meso-metathoracic sternite (Table 4b) with transverse slightly arched row of 5-7 bristles towards anterior margin—in 50 specimens, 24 per cent. with 5 bristles, 62 per cent. with 6, 14 per cent. with 7.

Abdomen : with short fine hairs uniformly scattered as on head ; with long strong bristles, truncated distally and slightly dilated apically, on 8th, 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate ; five such bristles on each side of almost equal length and longer than adjacent bristles, one of these on lateral margin of 8th tergite, two on lateral margin of 9th and two on lateral margin of 10th tergite, the bristle measured (Table 2) situated more dorsally on lateral margin of 9th tergite. Towards base of epiproct on each side of mid-line a bristle (Table 2), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 9th tergite laterally. Tergites 1 and 2 (in stained preparations) uniformly sclerotized or each showing a slight indication of division into two transverse bands. In freshly killed and stained specimens, 6th, 7th and 8th tergites with anterior and posterior transverse bands, the posterior band of 8th tergite divided medially by a colourless area ; remaining tergites uniformly sclerotized.

Body length 0.88-0.96 mm. (20 measurements). Various body measurements are given in Tables 2, 3, 4b.

Liposcelis pubescens sp. n. (fig. 5 and Pl. 1, fig. 6).

Female. Colour : Body semi-transparent. Upperside : shiny brown ; thorax and abdomen Mummy Brown ; cranium slightly more yellowish ; red pigment granules scattered sparsely and irregularly on head, very few on thorax and abdomen, those present almost completely masked by dark brown pigment of cuticle ; clypeus reddish ; eyes black ; antennae, maxillary palpi and tarsi almost colourless ; legs as abdomen ; terminal three segments of maxillary palpi, antennal segments 2, 3, 4 and sometimes 5, proximal tarsal segment and tibiae distally with large red pigment granules ; abdominal tergites 3-7 inclusive each divided into two transverse bands, the anterior one Mummy Brown, the

posterior one much narrower, lighter and visible when abdomen distended; anterior borders of tergites 3-8 inclusive each with a very narrow transverse dark brown medial streak less than half as long as width of abdomen. Underside: uniformly glossy Buffy-Brown; mouth parts more reddish; red pigment granules sparsely scattered on head; larger red pigment granules scattered uniformly on pro- and meso-metathoracic sternites but absent on abdominal sternites. In some individuals the fat body is visible as small lighter brown irregular patches in head, thorax and abdomen.

Sculpturing (Pl. 1, fig. 6): head dorsally with distinct arched ridges enclosing smooth spindle-shaped areas; abdominal tergites as head but with spindle-shaped areas more elongate and with some tubercles laterally. Epicranial suture indistinctly indicated by a slight break in the sculpturing in some individuals but absent in others.

Head: with fine hairs longer and more dense than those of *L. liparus*; length of hairs almost three times width of adjacent spindle-shaped areas on cuticle, distance between hairs equal to or less than length of hairs. Third antennal segment with 13-15 annular ridges (Table 3)—in 20 specimens, 5 with 13, 8 with 14, 7 with 15 annular ridges. Eye with 7 ommatidia (Table 3)—in 30 eyes, 100 per cent. with 7 ommatidia, their arrangement constant.

Thorax: with fine hairs uniformly scattered as on head; with 4-6 stronger and longer bristles, truncated distally, on prothorax laterally on each side (fig. 5), one on lateral tip ("humeral seta," Table 1), the others shorter and thinner and, with humeral seta, forming a transverse row half-way between anterior and posterior margins, with 2-4 small fine hairs more posteriorly near humeral seta. Prothoracic sternite (Table 4a) with 3-5 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 52 per cent. with 3 bristles, 46 per cent. with 4, 2 per cent. with 5. Meso-metathoracic sternite (Table 4a) with transverse slightly arched row of 6-9 bristles towards anterior margin—in 50 specimens, 10 per cent. with 6 bristles, 48 per cent. with 7, 38 per cent. with 8, 4 per cent. with 9.

Abdomen: with fine hairs uniformly scattered as on head; with long strong bristles truncated distally and dilated apically, on 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; two such bristles on each side of almost equal length and longer than adjacent bristles, both these situated on lateral margin of 10th tergite, the bristle measured (Table 1) being the more dorsal one of this pair. Towards base of epiproct on each side of mid-line a bristle (Table 1), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 10th tergite laterally. In freshly killed specimens and less distinctly in stained preparations, 1st tergite divided into five areas and 2nd tergite divided into two transverse bands as in *L. granicola* (fig. 2); remaining tergites uniformly sclerotized except for differentiation into anterior and lighter posterior transverse bands (*vide colour*).

Body length 1.06-1.21 mm. (30 measurements). Various body measurements are given in Tables 1, 3, 4a.

ENGLAND: on dusty shelves and old paper, Biological Field Station cellar, Slough, Bucks, 10th March, 1943 (type locality); on walls, Millwall Central Granary, London, 16th April, 1943.

Male. Colour: Body semi-transparent. Upperside: shiny brown; thorax and abdomen Buffy-Brown with only slight differentiation in colour between anterior and posterior regions of abdominal tergites; head slightly more yellowish; clypeus reddish; eyes black; small red pigment granules scattered very sparsely and uniformly on head, thorax and abdomen; antennae, maxillary palpi and tarsi almost colourless; legs as abdomen; many red pigment granules on terminal three segments of maxillary palpi and on proximal tarsal segments, only a few on antennal segments 2-4 inclusive; anterior borders of abdominal tergites 4-7 inclusive each with a very narrow transverse indistinct dark brown medial streak less than half as long as width of abdomen. Underside: uniformly glossy Light Buff: mouth parts more reddish; red pigment granules sparsely scattered on head, larger granules scattered uniformly on pro- and meso-metathoracic sternites and on 1st

abdominal sternite, absent on remaining abdominal sternites. Unlike the females, the fat bodies of laboratory bred males are usually not evident except when preserved in alcohol.

Sculpturing: as female.

Head: with fine hairs, length of hairs and distance between them as female. Third antennal segment with 10-14 annular ridges (Table 3)—in 20 specimens, 1 with 10, 6 with 11, 7 with 12, 4 with 13, 2 with 14 annular ridges. Eye with 5 ommatidia (Table 3)—in 30 eyes, 100 per cent. with 5 ommatidia, their arrangement constant.

Thorax: with fine hairs uniformly scattered as on head; with 2-3 stronger and longer bristles, truncated distally, on prothorax laterally on each side, one on lateral tip ("humeral seta," Table 2), the others shorter and thinner and, with humeral seta, forming a transverse row half-way between anterior and posterior margins, with 2-3 small fine hairs more posteriorly near humeral seta. Prothoracic sternite (Table 4b) with 3-4 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 92 per cent. with 3 bristles, 8 per cent. with 4. Meso-metathoracic sternite (Table 4b) with transverse slightly arched row of 5-9 bristles towards anterior margin—in 50 specimens, 2 per cent. with 5 bristles, 52 per cent. with 6, 44 per cent. with 7, 2 per cent. with 9.

Abdomen: with fine hairs uniformly scattered as on head; with long strong bristles, truncated distally and slightly dilated apically, on 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; two such bristles on each side of almost equal length and longer than adjacent bristles, both these situated on lateral margin of 10th tergite; the bristle measured (Table 2) being the more dorsal one of this pair. Towards base of epiproct on each side of mid-line a bristle (Table 2), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 10th tergite laterally. In freshly killed specimens and less distinctly in stained preparations 1st tergite divided into five areas and 2nd tergite divided into two transverse bands as in *L. granicola* (fig. 2); remaining tergites uniformly sclerotized except for slight differentiation into anterior and lighter posterior transverse bands (*vide colour*), the posterior transverse band of 8th tergite interrupted medially by a colourless tract.

Body length 0.76-0.88 mm. (20 measurements). Various body measurements are given in Tables 2, 3, 4b.

Liposcelis subfuscus sp. n. (fig. 5 and Pl. 1, fig. 7).

Female. Colour: Body semi-transparent. Upperside: dull brown; thorax and abdomen Sayal Brown; cranium reddish-brown; clypeus reddish; eyes black; antennae maxillary palpi and tarsi almost colourless; legs as abdomen; abdominal tergites 3-7 inclusive each divided into two transverse bands, the anterior one Sayal Brown, the posterior one lighter brown and much narrower; anterior borders of tergites 3-8 inclusive each with a very narrow transverse dark brown medial streak about half as long as width of abdomen. Underside: shiny; thorax and abdomen greyish-brown; head more reddish. Red pigment granules completely absent except for a few very sparsely scattered on thoracic sternites. The fat bodies of laboratory bred individuals were never visible through the cuticle.

Sculpturing (Pl. 1, fig. 7): head dorsally with distinct arched ridges enclosing transverse spindle-shaped areas bearing indistinct minute tubercles; abdominal tergites as head but spindle-shaped areas more elongate and tubercles more distinct laterally. Epicranial suture indicated by a break in the sculpturing.

Head: with short fine hairs uniformly scattered, length of hairs slightly greater than width of adjacent spindle-shaped areas on cuticle, distance between hairs about twice length of hairs. Third antennal segment with 13-19 annular ridges (Table 3)—in 20 specimens, 5 with 13, 5 with 14, 7 with 15, 2 with 17, 1 with 19 annular ridges. Eye with 6-8 ommatidia (Table 3)—in 25 eyes, 1 with 6 ommatidia, 22 with 7 (the arrangement constant), 2 with 8 (from the same individual, the arrangement different in each).

Thorax: with short fine hairs uniformly scattered as on head; with one stronger and longer bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta," Table 1) and with 5-7 small fine hairs mainly posteriorly near humeral seta (fig. 5). Prothoracic sternite (Table 4a) with 3-5 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 40 per cent. with 3 bristles, 38 per cent. with 4, 22 per cent. with 5; 98 per cent. with a posterior pair of bristles mid-way between anterior row and posterior margin of sternite, 2 per cent. with one of these bristles lacking. Meso-metathoracic sternite (Table 4a) with transverse slightly arched row of 5-9 bristles towards anterior margin—in 50 specimens, 2 per cent. with 5 bristles, 22 per cent. with 6, 52 per cent. with 7, 18 per cent. with 8, 6 per cent. with 9.

Abdomen: with short fine hairs uniformly scattered as on head; with strong bristles, truncated distally and dilated apically, on 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate; two such bristles on each side of almost equal length and longer than adjacent bristles, both these situated on lateral margin of 10th tergite, the bristle measured (Table 1) being the more dorsal one of this pair. Towards base of epiproct on each side of mid-line a bristle (Table 1), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 10th tergite laterally. In freshly killed specimens (with lateral illumination) and in stained preparations 1st tergite divided into five distinct areas and 2nd tergite divided into two distinct transverse bands as in *L. granicola* (fig. 2); remaining tergites uniformly sclerotized except for differentiation into anterior and lighter posterior transverse bands on tergites 3-7 (*vide colour*).

Body length 1.02-1.16 mm. (80 measurements). Various body measurements are given in Tables 1, 3, 4a.

ENGLAND: in Orris root from Boots' Chemists, Slough, Bucks., given to me by Dr. O. W. Richards, 10th September, 1943 (type locality); in grain dust (N. Manitoba wheat) from walls and floor of Symon's Wharf, London, 18th May, 1944; on walls and floor, Millwall Central Granary, London, 16th April, 1943.

Male. Colour: Body semi-transparent. Upperside: shiny brown; thorax and abdomen Sayal Brown with only slight differentiation in colour between anterior and posterior regions of abdominal tergites 3-7 inclusive; head slightly more yellowish; clypeus more reddish; eyes black; antennae, maxillary palpi and tarsi colourless; legs as abdomen; anterior borders of abdominal tergites 3-8 inclusive each with a very narrow transverse dark brown medial streak about half as long as width of abdomen. Underside: uniformly glossy Light Buff; mouth parts more reddish. Red pigment granules completely absent except for a few very sparsely scattered on thoracic sternites. The fat body was never visible through the cuticle.

Sculpturing: as female.

Head: with short fine hairs, length of hairs and distance between them as female. Third antennal segment with 11-14 annular ridges (Table 3)—in 20 specimens, 3 with 11, 9 with 12, 7 with 13, 1 with 14 annular ridges. Eye with 5 ommatidia (Table 3)—in 20 eyes, 100 per cent. with 5 ommatidia, their arrangement constant.

Thorax: with short fine hairs uniformly scattered as on head; with one stronger and longer bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta," Table 2) and with 3-4 small fine hairs mainly posteriorly near humeral seta. Prothoracic sternite (Table 4b) with 2-5 bristles anteriorly arranged in a transverse arched row—in 50 specimens, 34 per cent. with 2 bristles, 56 per cent. with 3, 8 per cent. with 4, 2 per cent. with 5; 100 per cent. with a posterior pair of bristles mid-way between anterior row and posterior margin of sternite. Meso-metathoracic sternite (Table 4b) with transverse slightly arched row of 4-7 bristles towards anterior margin—in 50 specimens, 2 per cent. with 4 bristles, 52 per cent. with 5, 44 per cent. with 6, 2 per cent. with 7.

Abdomen : with short fine hairs uniformly scattered as on head ; with strong bristles, truncated distally and slightly dilated apically, on 9th and 10th tergites laterally, on epiproct, paraprocts and subgenital plate ; two such bristles on each side of almost equal length and longer than adjacent bristles, both these situated on lateral margin of 10th tergite, the bristle measured (Table 2) being the more dorsal one of this pair. Towards base of epiproct on each side of mid-line a bristle (Table 2), truncated distally, much longer than adjacent bristles on epiproct but shorter than the two bristles on 10th tergite laterally. In freshly killed specimens (with lateral illumination) and in stained preparations 1st tergite divided into five distinct areas and 2nd tergite divided into two distinct transverse bands as in *L. granicola* (fig. 2) ; remaining tergites uniformly sclerotized except for differentiation into anterior and lighter posterior transverse bands on tergites 3-7 (*vide colour*), a very narrow or no posterior transverse band on 8th tergite.

Body length 0.76-0.90 mm. (10 measurements). Various body measurements are given in Table 2, 3, 4b.

Liposcelis granicola Broadhead and Hobby, 1944² (fig. 5, and Pl. 1, figs. 3, 8).

The following notes and the measurements given in the Tables are based on a study of the type and paratypes and supplement the original description.

Female. Colour : a few red pigment granules sparsely scattered on head and thoracic tergites and sternites.

Sculpturing (Pl. 1, figs. 3 and 8) ; head dorsally with transverse spindle-shaped areas enclosing distinct minute tubercles, the areas separated by plain narrow tracts bordered by rows of tubercles, tubercles forming anterior margins of areas partially fused, thus approaching the ridged condition in head of *L. luridus* ; abdominal tergites as head but spindle-shaped areas more elongate and tubercles on posterior margin of areas partially fused. Epicranial suture indicated by a break in the sculpturing.

Head : with short fine hairs uniformly scattered, length of hairs and distance between them as in *L. subfuscus*.

Thorax : with one bristle, truncated distally, on lateral tip of prothorax on each side ("humeral seta," Table 1) and with 2-3 small fine hairs almost as long more posteriorly near humeral seta (fig. 5).

Abdomen : with two bristles, truncated distally and dilated apically, on each side of almost equal length and slightly longer than adjacent bristles on apical abdominal segments, both these situated on lateral margin of 10th tergite, the bristle measured (Table 1) being the more dorsal one of this pair. Towards base of epiproct on each side of mid-line a bristle (Table 1) truncated distally and very dilated apically. 1st tergite divided into five areas (sometimes seven), 2nd tergite into two transverse bands (fig. 2).

Body length 0.96-1.08 mm. (50 measurements). Various body measurements are given in Tables 1, 3, 4a.

Parthenogenetic. No males.

² I have recently examined the paratypes of *L. divergens* Badonnel, 1943, which prove to be conspecific with *granicola*. *Granicola* must therefore fall as a synonym of *divergens*. Badonnel (1946, *Rev. Zool. Bot. afr.* 39 (2) : 143) now regards *divergens* as a synonym of *L. bostrychophilus* Badonnel, 1931.

TABLE 1.

Female. Linear measurements of ten characters of five *Liposcelis* species.

	N.	Mean (mm.)	Standard deviation	Extremes		Species
Width of head capsule	50	0.255	0.008	0.236	0.274	<i>granicola</i>
	30	0.263	0.005	0.251	0.270	<i>subfuscus</i>
	30	0.280	0.004	0.267	0.287	<i>pubescens</i>
	20	0.271	0.006	0.256	0.280	<i>luridus</i>
	20	0.276	0.006	0.266	0.291	<i>liparus</i>
Antennal length ...	50	0.541	0.023	0.489	0.581	<i>granicola</i>
	20	0.635	0.019	0.599	0.678	<i>subfuscus</i>
	20	0.675	0.017	0.640	0.705	<i>pubescens</i>
	21	0.839	0.033	0.773	0.882	<i>luridus</i>
	20	0.772	0.021	0.715	0.803	<i>liparus</i>
Length of 4th antennal segment	20	0.047	0.002	0.042	0.050	<i>granicola</i>
	20	0.054	0.002	0.051	0.060	<i>subfuscus</i>
	20	0.058	0.003	0.050	0.063	<i>pubescens</i>
	20	0.072	0.005	0.061	0.082	<i>luridus</i>
	20	0.068	0.004	0.061	0.075	<i>liparus</i>
Greatest width of hind femur	20	0.134	0.007	0.118	0.145	<i>granicola</i>
	20	0.149	0.005	0.135	0.155	<i>subfuscus</i>
	20	0.164	0.005	0.152	0.178	<i>pubescens</i>
	30	0.161	0.006	0.147	0.172	<i>luridus</i>
	20	0.158	0.006	0.149	0.170	<i>liparus</i>
Length of humeral seta	20	0.014	0.001	0.011	0.015	<i>granicola</i>
	20	0.021	0.001	0.019	0.024	<i>subfuscus</i>
	20	0.033	0.002	0.031	0.036	<i>pubescens</i>
	20	0.029	0.001	0.026	0.031	<i>luridus</i>
	20	0.042	0.002	0.037	0.045	<i>liparus</i>
Length of longest apical abdominal bristle ³	20	0.039	0.002	0.036	0.043	<i>granicola</i>
	20	0.056	0.002	0.053	0.060	<i>subfuscus</i>
	20	0.080	0.002	0.076	0.083	<i>pubescens</i>
	20	0.068	0.001	0.066	0.071	<i>luridus</i>
	20	0.095	0.003	0.088	0.101	<i>liparus</i>
Length of bristle on epiproct	20	0.027	0.002	0.024	0.030	<i>granicola</i>
	20	0.046	0.002	0.042	0.050	<i>subfuscus</i>
	20	0.067	0.002	0.062	0.072	<i>pubescens</i>
	20	0.048	0.002	0.044	0.051	<i>luridus</i>
	20	0.162	⁴	0.135	0.189	<i>liparus</i>
Length of proximal hind tarsal segment	20	0.071	0.002	0.067	0.074	<i>granicola</i>
	20	0.075	0.002	0.070	0.078	<i>subfuscus</i>
	20	0.082	0.002	0.077	0.085	<i>pubescens</i>
	20	0.096	0.002	0.092	0.100	<i>luridus</i>
	20	0.095	0.003	0.090	0.102	<i>liparus</i>
Length of second hind tarsal segment	20	0.038	0.001	0.036	0.040	<i>granicola</i>
	20	0.036	0.001	0.033	0.038	<i>subfuscus</i>
	20	0.038	0.001	0.036	0.040	<i>pubescens</i>
	20	0.041	0.001	0.039	0.043	<i>luridus</i>
	20	0.037	0.001	0.034	0.040	<i>liparus</i>
Length of distal hind tarsal segment	20	0.047	0.002	0.043	0.049	<i>granicola</i>
	20	0.045	0.001	0.042	0.046	<i>subfuscus</i>
	20	0.046	0.001	0.043	0.048	<i>pubescens</i>
	20	0.048	0.001	0.046	0.050	<i>luridus</i>
	20	0.047	0.001	0.045	0.049	<i>liparus</i>

³ Position of this bristle specified in descriptions.⁴ This measurement excludes curvature; standard deviation thus omitted.

TABLE 2.

Male. Linear measurements of ten characters of four *Liposcelis* species.

	N.	Mean (mm.)	Standard deviation	Extremes		Species
Width of head capsule	30	0.200	0.003	0.196	0.207	<i>subfuscus</i>
	30	0.209	0.005	0.204	0.214	<i>pubescens</i>
	20	0.197	0.005	0.186	0.206	<i>luridus</i>
	20	0.201	0.003	0.194	0.208	<i>liparus</i>
Antennal length ...	20	0.558	0.019	0.517	0.593	<i>subfuscus</i>
	20	0.581	0.023	0.511	0.619	<i>pubescens</i>
	21	0.745	0.028	0.677	0.792	<i>luridus</i>
	20	0.628	0.015	0.600	0.646	<i>liparus</i>
Length of 4th antennal segment	20	0.042	0.001	0.040	0.046	<i>subfuscus</i>
	20	0.048	0.003	0.042	0.054	<i>pubescens</i>
	20	0.062	0.004	0.054	0.069	<i>luridus</i>
	20	0.051	0.003	0.046	0.060	<i>liparus</i>
Greatest width of hind femur	20	0.112	0.004	0.107	0.117	<i>subfuscus</i>
	20	0.123	0.005	0.114	0.131	<i>pubescens</i>
	20	0.114	0.005	0.104	0.123	<i>luridus</i>
	20	0.117	0.006	0.104	0.128	<i>liparus</i>
Length of humeral seta	20	0.018	0.002	0.015	0.022	<i>subfuscus</i>
	20	0.027	0.001	0.024	0.029	<i>pubescens</i>
	20	0.022	0.002	0.019	0.025	<i>luridus</i>
	20	0.030	0.002	0.025	0.032	<i>liparus</i>
Length of longest apical abdominal bristle ⁵	20	0.058	0.002	0.055	0.062	<i>subfuscus</i>
	20	0.071	0.003	0.065	0.076	<i>pubescens</i>
	20	0.064	0.004	0.058	0.070	<i>luridus</i>
	20	0.080	0.006	0.071	0.090	<i>liparus</i>
Length of bristle on epiproct	20	0.040	0.002	0.036	0.045	<i>subfuscus</i>
	20	0.057	0.003	0.052	0.062	<i>pubescens</i>
	20	0.042	0.002	0.037	0.046	<i>luridus</i>
	20	0.124	0.002	0.114	0.141	<i>liparus</i>
Length of proximal hind tarsal segment	20	0.059	0.002	0.056	0.062	<i>subfuscus</i>
	20	0.060	0.002	0.057	0.065	<i>pubescens</i>
	20	0.072	0.002	0.070	0.076	<i>luridus</i>
	20	0.069	0.002	0.066	0.072	<i>liparus</i>
Length of second hind tarsal segment	20	0.031	0.001	0.030	0.034	<i>subfuscus</i>
	20	0.031	0.001	0.030	0.033	<i>pubescens</i>
	20	0.034	0.001	0.033	0.037	<i>luridus</i>
	20	0.031	0.001	0.030	0.033	<i>liparus</i>
Length of distal hind tarsal segment	20	0.038	0.001	0.036	0.039	<i>subfuscus</i>
	20	0.038	0.001	0.036	0.040	<i>pubescens</i>
	20	0.041	0.001	0.039	0.045	<i>luridus</i>
	20	0.040	0.001	0.037	0.042	<i>liparus</i>

⁵ Position of this bristle specified in descriptions.⁶ This measurement excludes curvature; standard deviation thus omitted.

Footnote to Tables 1 and 2.

For width of head capsule and antennal length of *granicola* 1 micrometer unit = 0.0009 and 0.0021 mm. respectively.

For these characters in the remaining species and for width of hind femur 1 micrometer unit = 0.0014 mm.

For other characters 1 micrometer unit = 0.0003 mm.

TABLE 3.

Number of annular ridges on 3rd antennal segment and number of ommatidia in five *Liposcelis* species.

Character	Female N.	Male N.	Species
Number of annular ridges on antennal segment 3	20 10-14	— —	<i>granicola</i>
	20 13-19	20 11-14	<i>subfuscus</i>
	20 13-15	20 10-14	<i>pubescens</i>
	20 14-20	20 13-19	<i>luridus</i>
	20 16-27	20 13-17	<i>liparus</i>
Number of ommatidia in each eye	20 6-7	— —	<i>granicola</i>
	25 6-8	20 5	<i>subfuscus</i>
	30 7	30 5	<i>pubescens</i>
	20 7	24 5	<i>luridus</i>
	32 5-7	20 4-5	<i>liparus</i>

TABLE 4.

Variation in chaetotaxy of pro- and meso-metathoracic sternites (the figures are percentages of individuals having the number of bristles indicated. 50 individuals of each sex and species examined).

(a) Female.

Species	Number of bristles on prothoracic sternite						Number of bristles on meso-metathoracic sternite						
	Anteriorly					Posteriorly	Anteriorly						
	3	4	5	6	7	1	2	5	6	7	8	9	10
<i>granicola</i>	54	42	4				100		2	42	32	24	
<i>subfuscus</i>	40	38	22				98	2	22	52	18	6	
<i>pubescens</i>	52	46	2						10	48	38	4	
<i>luridus</i>		38	34	22	6				2	48	28	16	6
<i>liparus</i>	14	80	6						2	74	24		

(b) Male.

Species	Number of bristles on prothoracic sternite					Number of bristles on meso-metathoracic sternite							
	Anteriorly				Posteriorly	Anteriorly							
	2	3	4	5	2	4	5	6	7	8	9		
<i>subfuscus</i>	34	56	8	2	100	2	52	44	2				
<i>pubescens</i>		92	8				2	52	44			2	
<i>luridus</i>		74	22	4				24	62	14			
<i>liparus</i>		96	4					10	56	34			

TABLE 5.

Liposcelis pubescens. Comparison of various measurements of wild caught females and females reared at 25° C. and 76% R.H. on yeast.

		Wild specimens N.		Laboratory reared specimens N.	
Width of head capsule ...	Mean	69	0.279	30	0.280
	Standard deviation		0.005		0.004
Greatest width of hind femur	Mean	74	0.165	20	0.164
	Standard deviation		0.006		0.005
Length of 4th antennal segment	Mean	59	0.061	20	0.058
	Standard deviation		0.002		0.003
Length of humeral seta ...	Mean	54	0.035	20	0.033
	Standard deviation		0.001		0.002
Length of bristle on epiproct	Mean	62	0.077	20	0.067
	Standard deviation		0.004		0.002
Length of longest apical abdominal bristle	Mean	67	0.087	20	0.080
	Standard deviation		0.004		0.002

Footnote to Table 5.

Wild caught sample : for width of head capsule and width of hind femur 1 micrometer unit=0.0009 mm. ; for other characters 1 micrometer unit=0.0002 mm.

DISCUSSION.

Colour : Reference has been made in all descriptions to Ridgway's colour nomenclature as a standard for comparison. Such comparison cannot be precise as the intensity of the colour of the cuticle varies with different light intensities and different magnifications and its texture differs from that of the charts. The colour itself, particularly that of the head capsule, also varies with the direction of the incident light. These difficulties have been overcome in part by examination of freshly killed animals against a white background at a magnification of 62 diameters and with an electric light source as near to the microscope stage as possible, the animal facing the light. Adjustment of the colour charts is then made to superimpose the image of the insect on to any particular colour of the chart. Under these conditions the most diagnostic colour characters are as follows :—

Females.

L. luridus is readily distinguished by its light yellow colour. Only small numbers of red pigment granules are present on the thorax and 1st abdominal segment laterally. There is no obvious differentiation of abdominal tergites 3-8 into two transverse bands such as are present in the other four species.

L. liparus may be recognised by its glossy and greasy appearance and by the much darker brown 8th, 9th and 10th abdominal tergites and subgenital plate. Large numbers of red pigment granules are present on the head, thorax and on all abdominal tergites laterally.

L. pubescens is much darker brown than *subfuscus* or *granicola*. The small brown sclerites on abdominal tergites 1 and 2 are less distinct than those of the two latter species and more red pigment granules are present on the head.

L. subfuscus and *L. granicola* are indistinguishable in colour. *L. granicola* varies in colour to some extent—some individuals appear greyer, others a duller brown, while some appear almost identical with individuals of *subfuscus*. Pigment granules are so few in both species as to be useless for identification.

Males.

L. luridus can be easily distinguished by its pale yellow colour and by the dense concentration of dark red pigment granules on the postero-lateral angles of the meso-metathorax and the lateral margins of the 1st abdominal tergite (fig. 3). Antennal segments 3–6 have large numbers of red pigment granules and are visibly dark red. Individuals vary in the strength of pigmentation and in some specimens these concentrations of pigment granules are not immediately obvious.

L. liparus has a glossy appearance. Large numbers of red pigment granules are present almost uniformly over the thorax and confined to a longitudinal band on the abdominal tergites laterally where they are more numerous than in the corresponding regions of *luridus* (fig. 6).

L. pubescens: on the head the pigment granules are more sparsely scattered than in *liparus* and *luridus*. It has fewer pigment granules on the abdomen than *liparus* and is much darker brown than *subfuscus*.

L. subfuscus: the small sclerites in abdominal tergites 1 and 2 are clearly visible when the illumination is lateral, these being more obscure in the other three species. It has extremely few pigment granules on the head or none at all, and such granules are completely absent on thorax and abdomen, whereas the pigment granules of *pubescens* are sparsely scattered on head, thorax and on the abdomen antero-laterally.

Sculpturing.

The sculpturing has been described from an examination at high magnifications of permanent balsam mounts of animals treated with KOH and stained deeply with acid fuchsin. Only the head dorsally and the abdominal tergites differ in their sculpturing to any appreciable extent, and these are distinct in each of the five species described here. The sculpturing alone cannot, however, be used as a diagnostic character as it is almost identical in some species—viz., *L. luridus* and *L. bakeri* Pearman. It may be remarked that in *liparus* and *luridus* the sculpturing of the head dorsally differs appreciably from that of the abdominal tergites, this not being true of the other three species.

Other Characters.

The very long fine curved hair on the epiproct is peculiar to *L. liparus*, the other four species having shorter bristles, straight and truncated distally, in this position. The pubescence of the head is distinct in

L. pubescens. In this species the hairs are separated from each other by a distance equal to or slightly less than their length. The hairs are much further apart in the other four species, but *pubescens* is almost identical in this respect with other known species, notably *L. bakeri*, which species, however, has tubercles on the head as in *luridus*, whereas these are completely absent on the head in *pubescens*. The number and grouping of the longest apical abdominal bristles separate the five species into two groups. *L. liparus* and *luridus* have on each side of the terminal abdominal segments five long subequal bristles, truncated distally, one on the lateral margin of the 8th tergite, two on the lateral margin of the 9th, and two on the lateral margin of the 10th tergite, these bristles being longer than their neighbours. *L. pubescens*, *subfuscus* and *granicola* have two such bristles on each side, both on the 10th tergite laterally. The presence of a posterior pair of bristles on the prothoracic sternite mid-

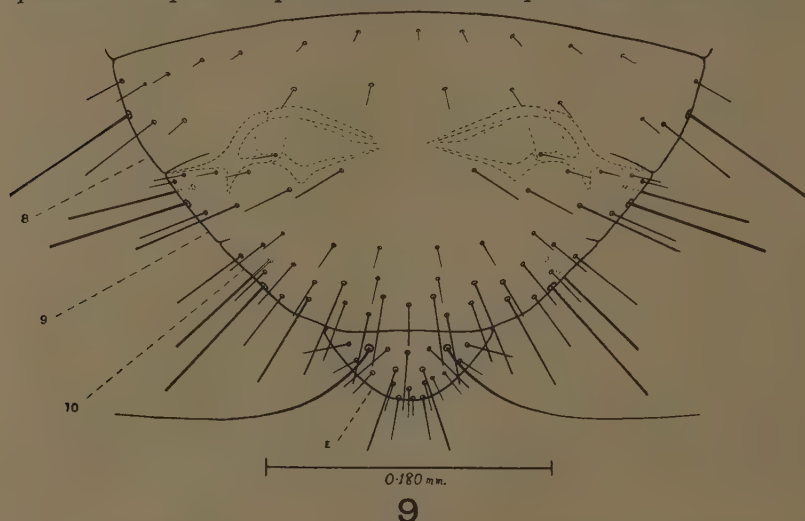


FIG. 9.—*L. liparus* ♀ dorsal view of terminal abdominal segments; 8, 9, 10, 8th, 9th and 10th tergites respectively; *E*, epiproct. Position of gonapophyses shown by broken lines.

way between the anterior row of bristles and the posterior margin of the sternite in *L. subfuscus* and *granicola* separates these species from *liparus*, *luridus* and *pubescens*, in which species these bristles are absent. The number of bristles on the prothorax laterally near the humeral seta is distinct in some of the species, although subject to some variation. Fig. 5 shows the most common arrangement in the females of each species.

The three characters—number of annular ridges on antennal segment 3, number of ommatidia and the chaetotaxy of the thoracic sternites—present so much variation within the species and so much overlap between species as to make them very unreliable for specific determina-

tion. The last two have been regarded as valuable diagnostic characters even without adequate statistical treatment in nearly all hitherto described species.

Linear Measurements.

There is a considerable overlap between the extreme measurements of any one character for species adjacent in size. This applies to all the characters in the male and to all the characters in the female except the length of the humeral seta and the length of the longest apical abdominal bristle. Nevertheless, with the exception of the lengths of the hind tarsal segments, the mean measurements of any one character differ significantly in the five species. Excluding the 2nd and 3rd hind tarsal segments, *L. granicola* is consistently the smallest species, and the male and female of *subfuscus* are consistently smaller than the males and females respectively of *liparus*, *luridus* and *pubescens*. These last three species, however, do not show any consistent gradation of size. Body length has not been treated statistically as the animals are soft and delicate and may contract or expand on killing. In each species there is a close correspondence between the two sexes in respect of the relative lengths and the magnitude of the difference between mean lengths of each of the ten characters, this being most marked in the length of the apical abdominal bristle.

The data presented in Tables 1 and 2 do not permit any exact comparison of variability. Coefficients of variability $\frac{(100\sigma)}{M}$ calculated for these data range from 1.86–7.00, but statistical comparison indicates that the differences of the coefficients between the two sexes is only doubtfully significant in some cases and not significant in others. Moreover in some of the former cases the female coefficient is the larger, in others the male.

It may be noted that all the above data refer to animals reared in the laboratory on yeast at 25° C. and 76% R.H. Comparison with a sample from a wild population has been possible in one instance. Measurements of six characters of female *L. pubescens* caught in a box of old papers in the cellar of the Biological Field Station, Slough, on 12th September, 1945 (type locality) are given in Table 5, together with the corresponding measurements of the laboratory reared animals. These females were individually identified by the colour of the insect and the hairiness and sculpturing of the head. The means and standard deviations of the two samples have been compared statistically for each character (comparing means : difference between means divided by

$\left(\sqrt{\frac{\sigma_1^2}{N_1} + \frac{\sigma_2^2}{N_2}}\right) > 3$ has been regarded as a significant difference ;

comparing standard deviations : a ratio of the square of the greater standard deviation to the square of the lesser standard deviation exceeding the critical value given in the variance ratio table at a 5 per cent. probability level has been regarded as a significant difference.) The means of width of head capsule and greatest width of hind femur do not

differ significantly between wild caught and laboratory reared samples. The difference between means is significant in the remaining characters. The differences between standard deviations are significant in the case of the apical abdominal bristle and the bristle on the epiproct, but are not significant in the remaining four characters. Since the two samples were derived from the same locality the significant differences between the means in four of the characters are probably due to environmental conditions, the wild caught specimens being the larger. This may be due to food and temperature. The wild caught females had probably been feeding on small particles of organic debris and perhaps on the mould growing on the paper. Compared with other foods yeast has been shown to be highly nutritious for *L. granicola* (Broadhead and Hobby, 1944). It is probably more nutritious than the natural food of the wild specimens. If this is true both the food of the wild caught sample and the lower temperature of the cellar compared with the laboratory conditions would tend to produce slower growth and reproductive rate than in the cultures, with an increase in size of some parts of the animal at any rate. As the widths of head capsule and hind femur have not been affected in the same way as the other characters these two must be regarded as more reliable measurements for taxonomic purposes than the others. Moreover these two characters are much larger than the others so that mechanical errors in measurement will be relatively less important. The fact that no significant differences between standard deviations occur in four of the six characters indicates that the rearing of a culture from a single wild caught female has had little appreciable effect on the variability as estimated from a sample from subsequent generations.

SUMMARY.

1. *Liposcelis liparus*, *luridus*, *pubescens* and *subfuscus* spp. n. are described with statistical observations of thirteen characters.

2. Specific characters of these four species and *L. granicola* Broadhead and Hobby are discussed.

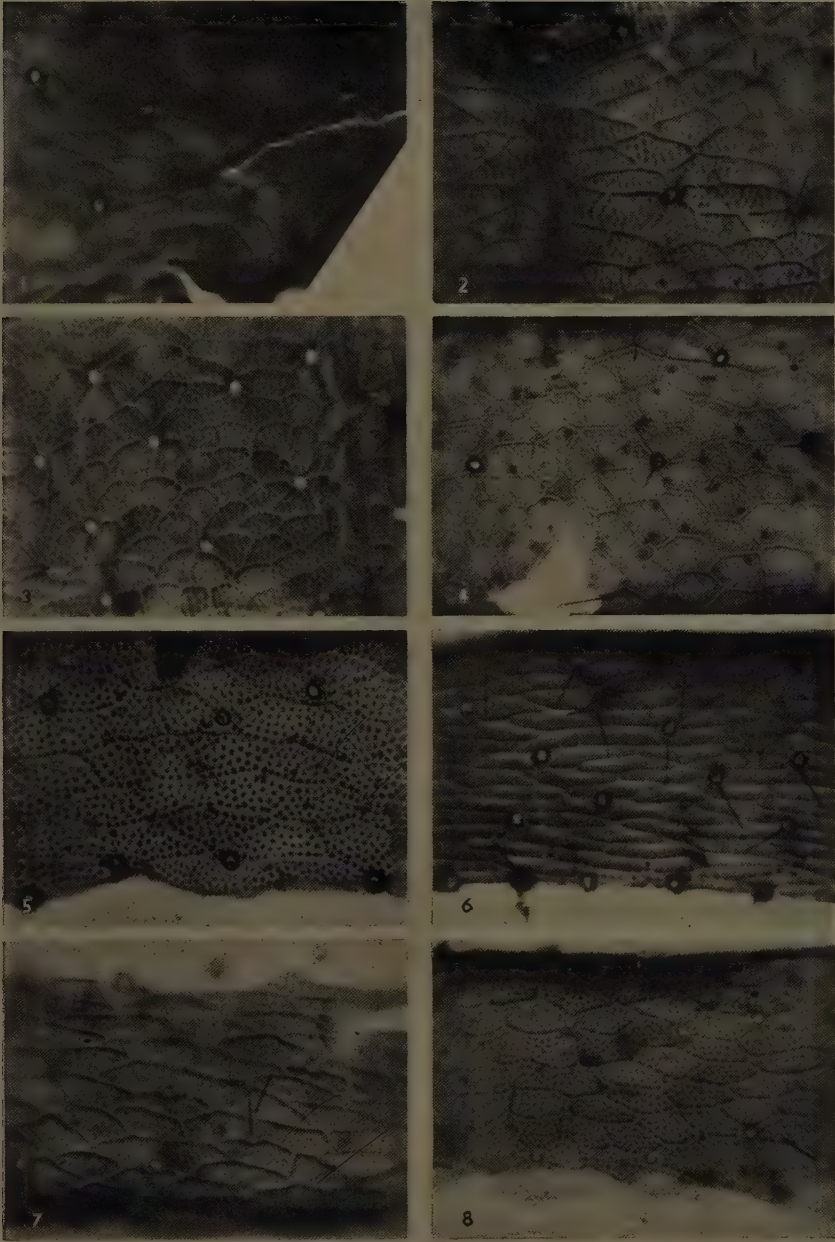
3. Comparison has been made between a sample of wild caught *L. pubescens* and a sample of laboratory bred animals of this species (type and paratypes) reared from a single fertilised female on yeast at 25° C. and 76% R.H.

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- RIDGWAY, R., 1912, *Color standards and color nomenclature*, Washington, D.C.

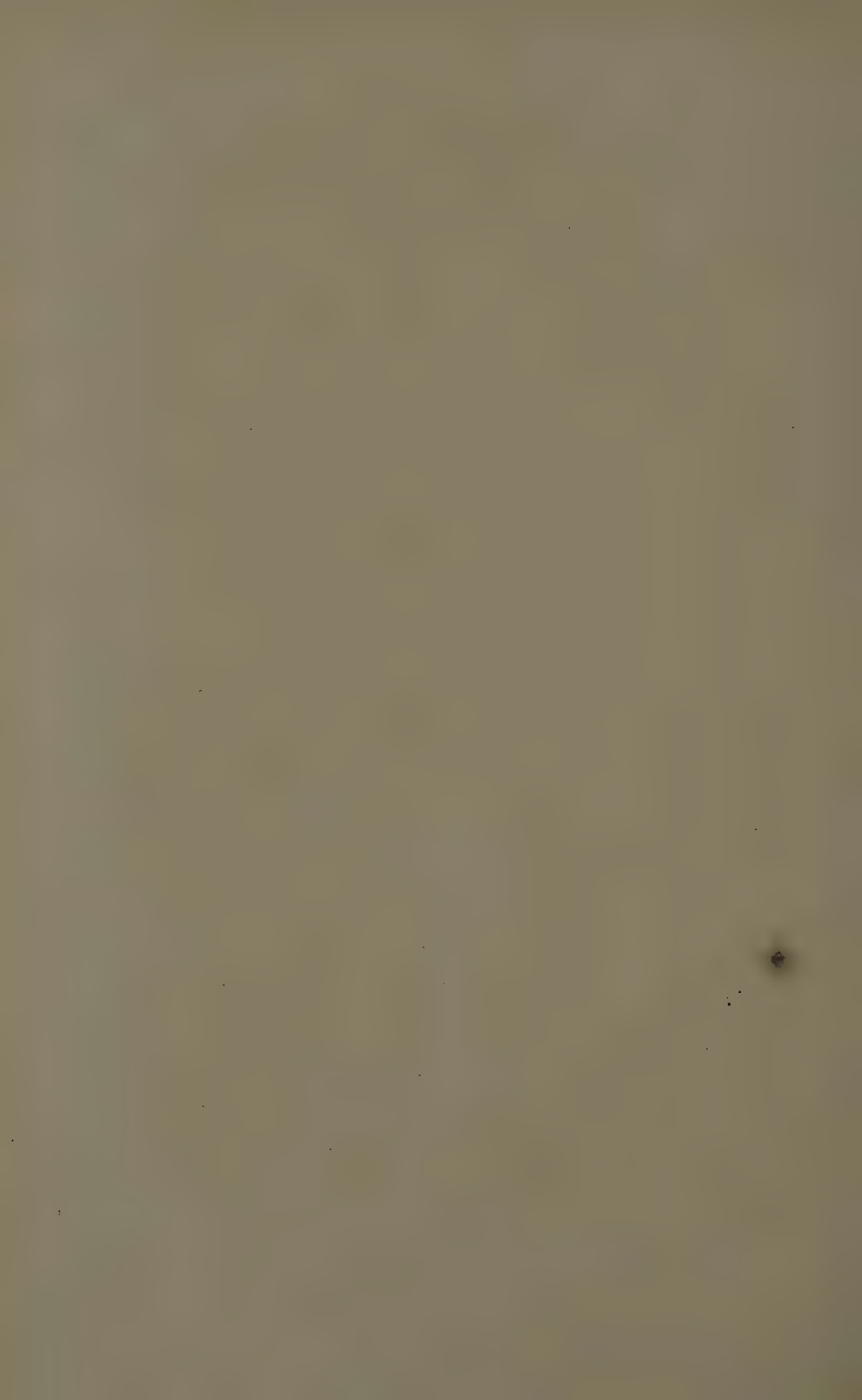
EXPLANATION OF PLATE 1.

FIGS. 1–8.—♀ cuticle to show sculpturing ; 1, *L. liparus* head dorsally ; 2, *L. luridus* head dorsally showing fork of epicranial suture ; 3, *L. granicola* head dorsally ; 4, *L. liparus* abdominal tergite ; 5, *L. luridus* abdominal tergite ; 6, *L. pubescens* abdominal tergite ; 7, *L. subfuscus* abdominal tergite ; 8, *L. granicola* abdominal tergite.



0·075 mm.

Cuticular sculpturing in *Liposcelis*.



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the NOCTUIDAE—III 59—90, 34 figs.

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ON THE LARVAE OF THE NOCTUIDAE—III

BY J. C. M. GARDNER, C.I.E., F.R.E.S.

(Forest Research Institute, Dehra Dun, U.P., India.)

Manuscript received 14th June, 1946.

(Read 6th November, 1946.)

WITH THIRTY-FOUR TEXT-FIGURES.

DIVISION B.

THIS Division consists of larvae in which the third abdominal segment bears abruptly reduced prolegs (as compared with those of A 5) or no prolegs at all; in *Abrostola*, however, the prolegs of A 3 are not very strongly reduced, but any doubt as to inclusion here will be removed by examination of the crochets, which are biordinal as in *Plusia*. This is to some extent an arbitrary arrangement since, although most genera of CATOCALINAE and NOCTUINAE are included, a few come into Division C in which the ventral prolegs are equal or only gradually reduced from A 6 to A 3. The prolegs of segment A 4 vary from absent to nearly equal to those of A 5.

Setal group VII on the first abdominal segment (A 1) is nearly always trisetose but is bisetose in some species of PLUSIINAE and almost certainly in *Rhesala imparata*. In *Erygia* one of the normal three setae of VII of both A 1 and A 2 is replaced by a sharply defined circle which is larger than the normal setal ring and has no seta. In *Bamra* and *Lacera* (fig. 17) similar circles replace VIII on A 1 and A 2.

Secondary setae are usually absent, but in G. 5689 the head and body have a close covering of short secondaries; in *Anomis*, *Cosmophila*, *Plecoptera* and some species of *Autoba* there is a quite long additional paradorsal seta on each side of the anterior abdominal segments. The usual number of setae on the ventral prolegs is three external and one internal; but in *Ischyja* there are numerous externals and in *Bamra*, *Nyctipao*, *Speiredonia* and *Thalatta* there are four externals.

Crochets are homoideous and usually uniordinal, but biordinal in PLUSIINAE and in *Ozarba*; usually simple but appendiculate in *Cosmophila*, *Marcillada* and genera of group B II.

Unusual characters are the pygidial projection in *Beana* and the ventrolateral fringe in *Erygia*.

In *Metachrostis trigona* the head is smaller in the final instar than in the preceding one and the mandibles of the two instars are very different.

Division B includes all larvae studied of the ERASTRIINAE, PLUSIINAE and HYPENINAE; some ACONTIINAE (as treated by Hampson, but this seems to be a heterogeneous subfamily); some CATOCALINAE and NOCTUINAE and, rather curiously, *Chasmina*, *Androlymnia* and *Elydna*

(*transversa* but not *reclusa*), which are treated as ACRONICTINAE by Hampson although they have no close relationship with that subfamily if my material is correctly identified.

Key to groups.

1. Crochets of prolegs on A 5, A 6 and A 10 are appendiculate. Prolegs of A 3 and A 4 either very small and equal or both absent B I
Without that combination of characters. If the crochets are appendiculate the prolegs of A 3 are absent, of A 4 well developed 2
2. Crochets biordinal. Prolegs of A 3 and A 4 reduced or absent. Spiracles not extremely small. Setae on distinct pimples. Seta III vertically above spiracle on A 8 (PLUSIINAE) B II
Crochets uniordinal except in *Ozarba*, in which the first seven pairs of abdominal spiracles are extremely small 3
3. Body setae on small but distinct basal pimples. Prolegs of A 3 absent or minute, of A 4 equal in length to those of A 5 and A 6. Spinneret attenuate. Seta III on A 8 nearly vertically above the spiracle (HYPENINAE) B II
Without that combination of characters. Spinneret not attenuate B IV

Group B I.

This group was discussed in Part I of this paper (1946, *Trans. R. ent. Soc. Lond.* 96 : 61-72). I have since found that appendiculate crochets are present in two other genera, *Cosmophila* and *Marcillada*, which, however, differ from B I in having the combination of no prolegs on A 3 and well-developed prolegs on A 4.

Group B II.

This group, treated in Part I of this paper (1946, *Trans. R. ent. Soc. Lond.* 96 : 61-72), consists of certain species belonging to the HYPENINAE and is sharply defined although some modification may be required to cover other genera of the subfamily. *Hypena auroincta* Hampson differs from larvae of other species *Hypena* in several ways and falls into Group B IV.

The following may be added to the previous characterisation :—

Ocellus 2 distinctly closer to 1 than to 3. On the first abdominal segment seta III is above the spiracle but slightly more caudad and seta V is directly below the spiracle or very nearly so. On A 1 and A 2 one of the three setae of VII is remote from the other two (which are approximate, their tubercles fused) and nearly level with VI.

Group B III.

This group consists of the PLUSIINAE as represented by *Plusia* and *Abrostola*.

Frons distinctly higher than wide, subequal in length to coronal suture. Ocellus 2 about half-way between 1 and 3. Labrum with small abrupt emargination. Mandible with sharp distal teeth and no internal tooth. Spinneret slender, nearly parallel sided, rounded apically; the triangular basal shield reaching about half-way. Labial palp with basal segment elongate; distal seta long. Prolegs either absent from A 3 and A 4 (*Plusia*) or present but distinctly narrower (*Abrostola*); in the first case minute single peglike projections may occur in the place of prolegs. Crochets very distinctly biordinal. Body setae rather long, on basal papillae which are usually rather weak but may be strong; III on A 8 is vertically above

the spiracle or very nearly so. Spiracles elliptical, that of A 7 rather more than half that of A 8. The skin with a covering of points varying from extremely fine to moderately large (visible with $\times 10$ lens). Pupae in leaves bound with silk.

It is a curious fact that setal group VII is bisetose in most of the larvae of *Plusia* examined, but is trisetose in specimens of *ni* and *nigrisigna*.

The PLUSIINAE seem well defined by the biordinal crochets and by the reduction of the two anterior pairs of prolegs. However, in *Ozarba* (group B IV) the crochets are biordinal and prolegs are missing from A 3 and A 4, but in this case the first seven abdominal spiracles are very small, that of A 7 less than half that of A 8.

Abrostola anophioides Moore.

Prolegs well developed on A 3 and A 4 but distinctly more slender than those on A 5 and A 6. Labral emargination about one-fourth deep, approximately right angled. Mandible with five fairly large and one small distal teeth. Penultimate segment of maxillary palp more than twice as long as wide and much longer than apical segment. Basal segment of labial palp three times as long as wide. Setiferous papillae of body setae small to moderate, but those bearing II on A 8 are larger, stoutly conical (fig. 1). The skin with extremely fine granulation that is only visible under high magnification. Length about 40 mm.

Head black laterally, pale medially, the frons sometimes blackish. Body pale, mottled with dark brown, sometimes with dark mediodorsal spots on A 1, A 2 and A 3. Spiracles pale with fine black rims. Legs dark testaceous. Larvae feeding on *Girardinia heterophylla*, Garhwal (Balwant Singh).

Plusia Ochsenheimer.

Prolegs absent from A 3 and A 4, at most represented by minute soft pegs. Crochets on other prolegs biordinal. Spiracles moderately large on A 1 to A 7. Body setae on pimples that are usually small but large in *peponis*.

Coloration is chiefly green, often with whitish lines; black marks and spots on head, body and legs do not appear to be constant within a species. Specific differences seem to be shown in the antenna, the two distal segments of the maxillary palp and in the microscopic clothing of the body skin.

The following notes are based on a few larvae of each species and require confirmation by examination of long series.

P. peponis Fabricius.

Distinguished from all others in having very strong erect tubercles bearing setae I and II on A 1 to A 4 and on A 8. Penultimate segment of maxillary palp distinctly longer than wide and much longer than distal segment. Body skin with not very close hairlike points. Larvae defoliate a creeper (CUCURBITACEAE); Dehra Dun.

P. ni Hübner.

Penultimate segment of maxillary palp about equal in length to distal segment and only slightly longer than wide. Skin points extremely small and dense, acute-granulate. VII on A 1 is trisetose in specimens seen. Larvae on *Antirrhinum*, cabbage and tomato; Dehra Dun.

P. nigrisigna Walker (figs. 2, 3, 4).

Distal segments of maxillary palp equal, the penultimate only slightly longer than wide. Antenna with basal segment transverse, the second about 1.5 times as long as wide. Skin points relatively large, visible with $\times 10$ lens. VII on A 1 trisetose in specimens examined. Larvae on *Cicer arietinum*; Dehra Dun and Cawnpore (Government Entomologist to U.P.).

P. orichalcea Fabricius.

Resembles *nigrisigna* but the skin-points are rather longer and VII is bisetose in specimens examined. The second antennal segment slightly more elongate. Larvae on *Brassica juncea* and *Dalbergia sissoo*; Dehra Dun.

P. jessica Butler.

Penultimate segment of maxillary palp nearly twice as long as distal segment and nearly three times as long as wide. Second antennal segment nearly three times as long as wide; basal segment longer than wide. Skin points fine, hair-like, not very dense. Larvae on unidentified weed; Dehra Dun.

P. albostrata Bremer and Gray.

Penultimate segment of maxillary palp about 1.5 times as long as second, nearly twice as long as wide. Second antennal segment elongate. Skin points extremely small. Larvae on *Dichrocephala latifolia*; Dehra Dun.

P. chalcites Esper.

Penultimate segment of maxillary palp nearly twice as long as second and rather more than twice as long as wide. Skin points extremely small, acuminate. Larvae on *Phaseolus mungo* and *Lantana camara*; Dehra Dun.

Group B IV.

This group includes the ERASTRIINAE (except *Amyna*, which has much in common with other genera of the subfamily but has been placed in B I on account of its combination of prolegs absent from A 3 and A 4 and crochets appendiculate on the other prolegs), several genera of CATOCALINAE and NOCTUINAE and *Hypena aurotincta* Hampson, the larval characters of which exclude it from subgroup B II which includes several other species of *Hypena*.

* Key to subgroups.

- | | |
|--|-------------------|
| 1. Prolegs absent from the third abdominal segment | 2 |
| Prolegs present on A 3 | B IV _c |
| 2. Prolegs absent from A 4 | B IV _a |
| Prolegs present on A 4 | B IV _b |

Group B IV_a.

(Prolegs absent from A 3 and A 4.)

Key to genera or species

- | | |
|---|-----------------------------|
| 1 Head and body with close covering of short secondary setae | G 5689 |
| Without secondary pubescence | 2 |
| 2. Adfrontal sutures extending to vertical sinus. (Legs and prolegs very short. Setae minute) | <i>Porphyrinia amabilis</i> |
| Adfrons not reaching vertical sinus | 3 |
| 3. Crochets biordinal | <i>Ozarba</i> spp. |
| Crochets uniordinal | 4 |
| 4. Some of the setae as long as the thickness of the body or longer. (III on A 8 vertically above the spiracle) | 5 |
| Setae shorter | 6 |

5. Some of the setae on anterior abdominal segments very long and resembling blades of grass. Setae on strong tubercles. Labral emargination about one-third deep. Larvae larger, about 50 mm. long *Tinolius* spp.
Body setae sometimes expanded and long but labral emargination shallow. Larvae up to about 25 mm. long *Autoba* spp.
6. Ocellus 2 not distinctly closer to 1 than to 3. Labral emargination very shallow 7
Ocellus 2 distinctly closer to 1 than to 3 or if nearly half-way between them the labral emargination is abrupt, about a third deep 9
7. Ocellus 2 very widely separated from 1, the interspace about twice that between 2 and 3 *Autoba angulifera*
Ocellus 2 half-way between 1 and 3 8
8. Seta III on A 8 is vertically above the spiracle *Tarache, Hoplotarache*
Seta III on A 8 is more cephalad *Lithacodia signifera*
9. Setal rings of II on A 8 flush with the skin. (Mandible with distal margin entire or only feebly dentate) 10
Setae II on A 8 on pimples which may be small 11
10. Head nearly as wide as high. Ocellus 2 very close to 1. Body depressed posteriorly *Mocis frugalis*
Head distinctly transverse. Ocellus 2 more widely separated from 1. Segment A 8 tumid above *Plusiodonta coelonota*
11. Labral emargination a wide shallow curve *Dinumma deponens*
Labral emargination abrupt 12
12. Mandible with internal tooth. (Smaller larvae up to 25 mm. long) *Hypera aurotincta*
Mandible without internal armature. (Length about 50 mm. or more) *Calesia, Pasipeda*

G. 5689.

Head and body closely covered with fine, rather short, secondary hairs which tend to hide the primaries which, however, are usually rather longer. Frontal setae low, but distinctly above the pores. Ocellus 2 well separated from 1 but slightly closer to it than to 3. Labral emargination obtuse, about a third deep, with straight sides. Mandible with three sharp apical teeth and without internal armature. Penultimate segment of maxillary palp wider than long. Basal segment of labial palp about twice as long as wide. Spinneret a little more than twice as long as wide, the apex broad, bilobed. Prolegs absent from A 3 and A 4. Setae not raised basally. Spiracles pale, of A 1 to A 7 moderately reduced. Body without projections of any kind. Length about 30 mm. The head is faintly yellow, the body skin colourless, a green tinge being due to the contents.

The larva feeds on leaves of *Bauhinia variegata*; Dehra Dun. Several moths were reared but have not been identified so far.

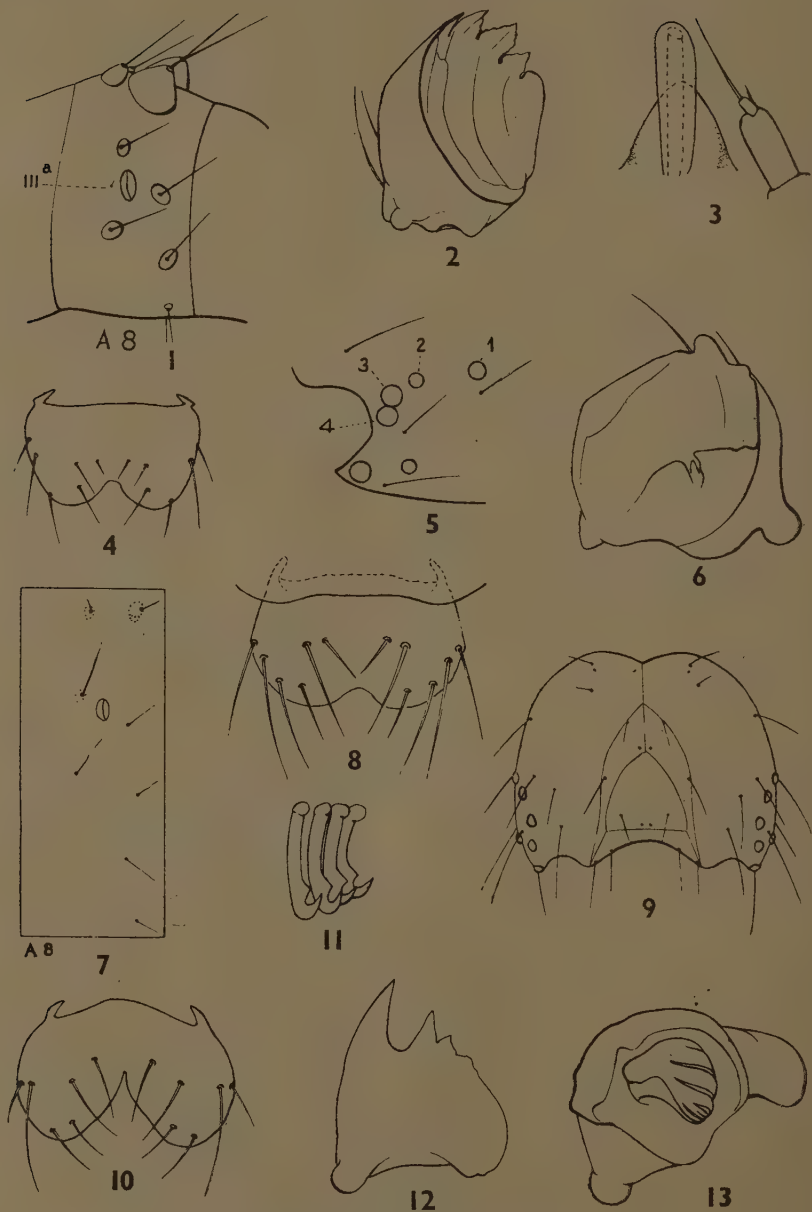
Porphyria amabilis Moore.

Gardner, 1941 : 272 (*Eublemma amabilis*).

This larva, predacious on the Lac Insect, is the only one known, other than certain species of *Agrotis* and *Euxoa*, in which the adfrontal sutures extend to the vertical sinus. The body setae are minute and the labrum is not distinctly emarginate.

Autoba Walker.

Two species, *A. olivacea* Walker and *A. silicula* Swinhoe were previously described under *Eublemma* (Gardner, 1941 : 272). Larvae of



For explanation of figures see page 89.

A. abrupta Walker and *A. angulifera* Moore have since been provided by Dr. K. S. P. Aiyar, Travancore. The four species have the following characters :—

Adfrontal sutures meeting well before vertical sinus. Labral emargination obtuse and shallow. Ocelli 1 and 2 widely separated. Mandible dentate distally, with no internal tooth. Spinneret rather slender, blunt apically. Legs of metathorax well separated. Small larvae up to about 25 mm. in length.

A. angulifera Moore.

Differs markedly from the other three in having only moderately long body setae (not as long as half the body thickness), in the remarkably wide separation of ocelli 1 and 2, the space between which is more than twice that between 2 and 3 (fig. 5), and in seta III on A 8 being very nearly directly anterior to the upper extremity of the spiracle. The spiracles oval, those of A 1 to A 7 about half that of A 8. Prolegs short. Setae on small plates (larger on T 2, T 3), the setal rings at most minutely raised. Head and pronotum uniformly testaceous, remainder of body pale green. Length about 18 mm. K. S. P. Aiyar (1943, *Indian J. Ent.* 5 : 53) describes the life history. The young larvae feed on the flowers of *Mangifera indica* and later, under cover, on the tender flower stems.

In *abrupta*, *olivacea* and *silicula* the setae are long, some of them longer than the body thickness ; ocellus 2 is about half-way between 1 and 3 and seta III on A 8 is vertically (or nearly so) above the spiracle. In *silicula* an extra paradorsal seta (seta x ?) is long ; in the other two it is short.

A. abrupta Walker.

Certain setae (e.g., on T 3 and II on A 1) strongly fusiform clavate (not merely flattened) and with long fine stalk. Setae on conical tubercles some of which, especially those bearing seta III on A 1 to A 4, are very large (IIIa small ?). Head infuscated laterally, the clavate setae dark brown. Described from a larva lacking most of the body setae (K. S. P. Aiyar ; Travancore).

A. olivacea Walker.

All setae simple, long, on small pimples. IIIa strong and approximate to III above spiracles. Spiracles A 1 to A 7 moderate, more than half that of A 8. Skin with dense minute skin points. Head rather coarsely granulate above.

A. silicula Swinhoe.

Setae simple, long, setae II and III on small pimples that are more evident towards the extremities of the body. IIIa rather long but not very close to III. Spiracles broadly oval, of A 1 to A 7 very small. Skin with minute skin points. Head finely irregular. This larva has been reported from flowers of mango and *Nyctanthes arbortristis*, also from the heads of several grain crops ; in this collection are larvae from witches broom on mango. I have recently found larvae abundantly present in the curled leaves of *Michelia champaca* seriously attacked by the aphid, *Prociphilus micheliae* Lambers, and it is suspected that the larva is predacious on the aphid, especially as no signs of its feeding on the leaf were apparent. The larva will, however, eat the leaf when given no choice.

Tarache Hübner, *Hoplotarache* Hampson.

The larvae of *T. marmoralis* Fabricius and *H. lunana* Fabricius were previously described (Gardner 1941 : 270). The labral emargination extremely obtuse and shallow. Ocellus 2 about half-way between 1 and 3. Mandible dentate apically and with large internal tooth. Setae short ; I and II on A 8 on small pimples ; III vertically above spiracle on A 8. Spiracles of A 1 to A 7 very small. Larvae on *Sida rhombifolia* (Malvaceae). Pupae in earthen cocoons firmly bound with silk.

Ozarba Walker.

Three species, *O. brunnea* Leech (Gardner, 1941 : 274), *O. punctigera* Walker and an unidentified species have the following larval characters :

Crochets biordinal. Spiracles of A 1 to A 7 extremely small, that of A 7 rather less than that of A 8 (a distinction from *Plusia* in which crochets are also biordinal). Labral emargination more abrupt than in other ERASTRIINAE examined, subacute and about a third deep in *brunnea*, more acute and nearly half deep in *Ozarba* sp. indet. Ocellus 2 not much closer to 1 than to 3. Mandible sharply dentate, with no internal tooth. Spinneret obtuse at apex. Body setae moderate, at most on minute pimples. III of A 8 not quite vertically above the spiracle. The three pairs of prolegs fairly long. Small slender larvae up to about 25 mm. long.

O. punctigera Walker has black and white stripes on the head, the body is dull brown with a white subspiracular line and some fainter pale lines above ; on grass, Dehra Dun. *O. brunnea* Leech is mostly pale green, with small black spots usually evident. Both species on grass ; Dehra Dun. Pupates in folded leaf.

Lithacodia signifera Walker.

Head wider than high. Frons higher than wide, the setae sublateral. Ocellus 2 equidistant from 1 and 3. Labral emargination a rather small but abrupt notch. Mandible with feeble distal angulations and traces of an internal ridge. Spinneret about three times as long as wide, parallel, broad at apex. Setae rather short, not on distinct pimples. Seta III on A 8 rather close to spiracle, higher and anterior. Spiracles oval, of A 1 to A 7 very small. Length about 18 mm. Pale green, spiracles pale. On grass ; Dehra Dun. Pupates in thin cocoon of silk and soil. .

Mocis frugalis Fabricius.

Head nearly as high as wide. Frons small, higher than wide ; the setae slightly above the pores, not near lateral margins. Ocellus 2 very close to 1, distant from 2 (fig. 22). Labral emargination slightly less than a curved right angle, about a fourth deep. Mandible with distal margin entire ; with a weak internal ridge. Spinneret about three times as long as wide, parallel sided, broadly rounded at apex. Setae mostly short, their bases flush with the skin. III on A 8 nearly level with upper extremity of spiracle. Spiracles moderate, of A 1 to A 7 rather more than half that of A 8. Length about 45 mm. Head dark brown with fine pale lines, a broader pale median line (including frons and adfrons) and two broader pale lines on each side ; body with fine dark and pale lines closely set ; a darker band along each side of dorsum and the ventral surface dark ; a very distinct transverse dorsal mark between A 1 and A 2 and between A 2 and A 3 ; legs and prolegs dark. Pupa in silk cocoon ; on grass.

Plusiodonta coelonota Kollar.

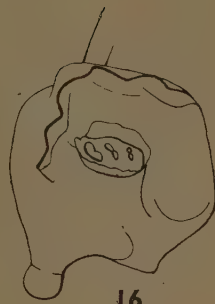
Head rather strongly transverse. Frons higher than wide, subequal in length to coronal suture ; convex ; the setae sublateral. Ocellus 2 slightly nearer to 1 than to 3. Labral emargination subacute, nearly one-third deep. Mandible with three rather obtuse distal teeth and a strong internal tooth. Spinneret about three times as long as wide, subparallel, broad apically. Setae mostly very short (rather longer on head and legs) not raised basally. Seta III on A 8 high above level of spiracle and more cephalad. A 8 is tumid above. Spiracles narrowly oval, of A 7 about half that of A 8. Length about 25 mm. Head reddish brown ; body fuscous greenish with pale patches and black marks ; spiracles with black rims. Larvae on *Cissampelos pareira* (MENISPERMACEAE). Pupa in elongate fusiform cocoon of earth loosely bound with silk.



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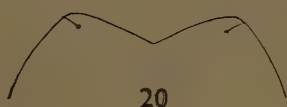
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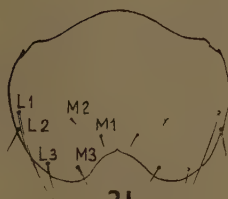
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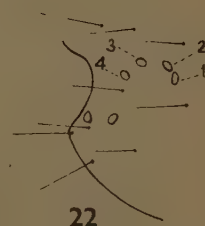
A B 19



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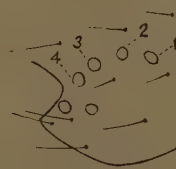
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For explanation of figures see page 89.

Dinumma deponens Walker.

Ocelli 1 to 4 rather close but 2 closer to 1 than to 3. Frons rather narrow, the frontal setae distant from lateral margins, slightly above level of pores. Labral emargination a shallow curve. Mandible with sharp distal teeth and a complex denticulate internal projection and a fairly large simple tooth. Spinneret about twice as long as wide, weakly tapering, bluntly rounded at apex. Setae rather short, on minute pimples which are rather larger (I, II) on A 8. Seta III on A 8 anterior to spiracle and very slightly above the level of its upper extremity. Length about 30 mm. Colour pale green, spiracles pale. Pupa with bloom; in leaves bound with silk. Larvae on leaves of *Albizia procera* (LEGUMINOSAE); Dehra Dun.

Tinolius Walker.

Prolegs absent from A 3 and A 4. Setae long and fine except that on at least the first abdominal segment; setae II and III are much longer, strongly flattened and pointed at the apex (resembling blades of grass); setae on tubercles, some of which are strong and conical on the upper surface; III on A 8 is directly above the spiracle. Head with frons higher than wide, the setae well above the pores and lateral. Labral emargination curved, about a third deep and rather abrupt. Mandible with three sharp, rather small apical teeth and with no internal armature. Ocellus 2 nearly half-way between 1 and 3.

I have seen only imperfect material of this genus. The exuviae of *T. quadrimaculatus* Walker (with a moth sent for identification by the Forest Entomologist, Burma) is mostly black with white marks above, but the prolegs red; the head black with a white line along coronal suture and dividing into two branches to base of mandibles; also a white lateral streak on each side posteriorly; ocellus 2 about half-way between 1 and 3. Blade shaped setae on first three abdominal segments. A larva of an unknown species sent by Dr. N. L. Bor from Assam has many setae missing, but apparently blade-shaped setae are limited to segment A 1; head testaceous with forked white line, the frons, adfrons and two spots on vertex black; body with black variegation on a pale ground; prolegs reddish; length 55 mm. The shrivelled remains of two larvae collected in Burma have the head coloured as in *quadrimaculatus*, and blade-shaped setae are present on A 1 to A 3 but smaller and paler (brown instead of blackish) on the last; prolegs black; body black with pale transverse bands intersegmentally. This may be *T. eburneigutta* Walker as figured in Moore, 1887, *Lep. Ceylon* 3, pl. 171.

Calesia Guenée, *Pasipeda* Walker.

Prolegs absent from A 3 and A 4. Frons higher than wide, not much shorter than coronal suture; frontal setae near lateral margins and distinctly above level of pores. Ocellus 2 very close to 1, more widely separated from 3. Labral emargination abrupt, rather less than right angled, curved at base and less than half deep. Mandible with three distal teeth, with no internal armature. Basal segment of labial palp elongate. Spinneret extending beyond second segment of labial palp, broadly rounded at apex. Body setae rather long, those on posterior segments at least, on distinct pimples; III close to spiracle, nearly directly anterior to its upper extremity. Spiracles black, of A 1 to A 7 rather more than half as large as that of A 8. Skin closely and microscopically granulate.

The three species of larvae available are very similar in structure, but one of them is distinguished by the fine pseudopubescence of the skin. The larvae, about 50 mm. long, favour plants of the ACANTHACEAE. Pupae without bloom; in folded leaves.

Pasipeda haemorrhoea Guenée.¹

Two sets of reared moths were at first identified as this species, certain differences being assumed to be sexual. However, on examining the larvae of each set a difference was found in the skin surface. It seems impossible to say from literature which is the true *haemorrhoea*.

Species "a" is distinguished by an extremely fine and short clothing of hair-like skin points (very distinct under high power) on the skin. Head pronotum and pygidium red, with black spots, body dark grey with thin black lines crossed by transverse lines on each segment; a large black spot dorsolaterally on A 1 to A 4. Setae white, on black spots. The fine skin points give a silky appearance. Length about 55 mm. On *Barleria cristata* (ACANTHACEAE). (The moths darker in colour; anal tubular tufts less developed; vein 7 from a little beyond the areole in fore-wing; antennae ciliated and not thickened.) *Species "b"* has no skin points. Head yellow with black spots and marks. Body yellow with broken lines and much close black mottling. Setae on quite distinct pimples that are fairly large on A 8 and A 9. On *Daedalacanthus nervosus* (ACANTHACEAE). (Moths a lighter brown; anal tuft large; vein 7 from the areole in fore-wing; antennae with four or five spines on slightly thickened basal fourth.)

Calesia dasyptera Kollar. (fig. 7).

Resembles the last (*species b*) in having no fine hair-like skin points and differs in the setal pimples being less developed and hardly visible on the first six abdominal segments. Head red with black spots; body slate grey with sparse fine black longitudinal and transverse (a few) black lines; reddish spots behind spiracles of abdomen. Larvae on a species of ACANTHACEAE.

Hypena aurotincta Hampson.

This species differs from the other species of *Hypena* examined (group B II) in having no prolegs on A 4; the setal rings are scarcely raised on the anterior segments but small pimples are present posteriorly, being more evident on A 8 and A 9; III on A 8, although above the level of the spiracle, is more cephalad than in the other species; the spinneret is obtuse at the apex; the frontal setae more removed from the margins of frons.

Ocellus 2 much closer to 1 than to 3. Labral emargination rather abrupt, about a third deep, widely curved at base. Mandible dentate, with internal armature as in fig. 59. Basal segment of labial palp slender, about twice as long as apical seta. Spiracle A 1 to A 7 very small, about half that of A 8. Setae moderately long. Body length about 35 mm.

Head almost colourless except for some vague brownish markings—body pale greenish with vague dark speckling; spiracles pale with black rims. Feeds on *Abrus precatorius* (LEGUMINOSAE). Pupa without bloom, in folded leaves.

¹ The two species referred to in this paragraph have been determined by the Imperial Institute of Entomology as *Calesia patna* Felder (Species "a") and *Calesia haemorrhoea* Guenée (Species "b"). *C. patna* has hitherto been considered to be a synonym of *haemorrhoea*, but examination of the types, in the light of Mr. Gardner's study of the larvae, shows them to be distinct.—T. H. C. TAYLOR.

Group B IVb.

(Prolegs absent from A 3, present on A 4.)

Key to genera or species.

1. Crochets (fig. 11) appendiculate. (Ocellus 2 about half-way between 1 and 3) 2
 Crochets simple 3
2. Frons distinctly higher than wide. Adfrons not very wide. An additional seta is distinct between II and IV on anterior abdominal segments *Cosmophila* spp.
 Frons scarcely higher than wide. Adfrons (fig. 9) very wide above. Abdomen without distinct additional setae *Marcillada rubricosa*
3. Frons about as high as wide, a nearly equilateral triangle. (Prolegs of A 4 very small) 4
 Frons distinctly higher than wide 5
4. Labral emargination more than half deep. Abdominal segments with an additional paradorsal seta on each side. *Plecoptera reflexa*
 Labral emargination weak and obtuse. Abdomen without such additional setae *Swinhoea vegeta*
5. Setae II of A 8 each on an abrupt conical tubercle. (Body setae on small dark plates) *Attonda adspersa*
 Seta II at most on small pimples 6
6. Prolegs of A 4 minute, scarcely protuberant. Ocellus 2 only slightly nearer 1 than 3. Small green larvae up to 20 mm. long *Hiccoda dosaroides*
 Without that combination 7
7. Ocelli 2 not closer to 1 than to 3 (Prolegs of A 4 about as long as those of A 5. Mandible dentate and with large internal tooth. Larvae up to about 20 mm. long) 8
 Ocelli 2 nearer 1 than 3 (only slightly so in *Oraesia* with a dull black, pale spotted head) 9
8. Setae not raised basally. Spiracle of A 8 not twice as large as that of A 7 *Rhesala imparata*
 Setae on small pimples. Spiracle of A 8 more than twice that of A 7 *Zethes pectinifer*
9. The three ventral pairs of prolegs nearly equal. (Pale green larvae up to about 19 mm. long. Mature (prepupal) larva without spots; mandible with one long and two shorter acute teeth. Preceding instar with black (setal) spots and mandible almost entire) *Metachrostis trigona*
 If the prolegs of A 4 are nearly as large as those of A 5, the larvae darker and 30 mm. or more in length 10
10. Ocelli 1 and 2 well separated. Head dull black with four small pale spots on each side *Oraesia* spp.
 Ocelli 1 and 2 very close together. Head colouring otherwise 11
11. Prolegs of A 5 and A 6 with four external setae. (Head nearly as high as wide. A 8 with strong dorsal hump) *Nyetipao crepuscularis*
 Prolegs of A 5 and A 6 with three external setae 12
12. Labral emargination shallow and obtuse (II on A 8 on very weak tubercles) *Grammodes stolidia*
 Labral emargination abrupt 13

13. Prolegs of A 4 very small. Frons small, very much shorter than coronal suture. A 8 not tumid . . . *Pericyma umbrina*
 Prolegs of A 4 about as long as those of A 5. Frons not much shorter than coronal suture. A 8 somewhat tumid above
Calpe minuticornis

Hiccoda dosaroides Moore.

Gardner, 1941 : 273.

Frons moderately higher than wide, the setae slightly above the pores. Ocellus 2 nearly half-way between 1 and 3. Labrum (fig. 8) only moderately transverse, the emargination very small, nearly semicircular. Mandible rounded distally, without distinct teeth; internal face with a patch of granules, without distinct tooth. Spinneret long and slender, rounded at apex. Apical segment of maxillary palp shorter than the elongate preceding segment. Setae rather short; not distinctly raised basally; III on A 8 anterior to spiracle and nearly level with its upper extremity. Prolegs of A 4 extremely small, only weakly protuberant. Spiracles of A 1 to A 7 minute, of A 7 less than half A 8. Length about 20 mm. Head and body pale green; spiracles pale with black rims. On grass.

Swinhoea vegeta Swinhoe.

Frons not much shorter than coronal suture, an almost equilateral triangle; setae nearly level with pores. Ocelli 1 to 4 rather close, 2 slightly nearer 1 than 3. Labral emargination obtuse and weak. Mandible with acute distal teeth, three large, four small; with no internal armature. Spinneret short, obtuse at apex. Body setae very short, the rings flush with the skin; III on A 8 anterior to spiracle. Prolegs of A 4 much smaller than those of A 5. Spiracles black, of A 8 nearly twice that of A 7. Length about 20 mm. Head fuscous with small white marks; body fuscous with some white marks, a broad white subspiracular band along the body; legs and prolegs fuscous. Pupa in cocoon of soil and silk. Larvae on *Ipomaea muricata*.

Cosmophila Boisduval.

I previously described (Gardner, 1941 : 287) the larvae of four species (*erosa* Hubner, *sabulifera* Guenée, *fulvida* Guenée, *mesogona* Walker) under *Cosmophila*, following Hampson (1926, PHALAEENAE : 345). It appears that only the first is a *Cosmophila*, the other three belonging to the distinct genus *Anomis*. Tams (1924, *Trans. ent. Soc. Lond.* 1924 : 24) has shown that *erosa* is limited to the New World although this name has been commonly used for two distinct Indian species, *C. flava* Fabricius and *C. lyona* Swinhoe.

In larvae of *Cosmophila* (*flava*, *lyona*) prolegs are absent from A 3 and the crochets of the other prolegs are appendiculate, whereas in *Anomis* (three species) reduced prolegs are present on A 3 and the crochets are simple. In both genera a strong additional seta is present between II and IV on the anterior abdominal segments.

Mature larvae. Frons higher than wide, the setae well above the pores. Ocellus 2 half-way between 1 and 3. Labral emargination nearly right angled, with straight sides, about a third deep. Mandible with rather weak distal teeth and with large internal plate-like ridge. Spinneret about three times as long as wide, parallel, obtuse. Setae moderately long, on small pimples. A strong additional seta present about half-way between II and IV on A 1 to A 6. Seta III on A 8 anterior to and above level of spiracle. Prolegs of A 4 much smaller than those of A 5. Crochets appendiculate (fig. 11). Spiracles rather narrowly oval, with fine black rims; of A 7 a little more than half that of A 8. Length about 30 mm.

Both *C. flava* Fabricius and *C. lyona* Swinhoe feed on MALVACEAE, including cotton. I have insufficient material to determine if specific differences are to be found. Colour mainly green. Pupa without bloom ; in loose cocoon in leaves or soil.

Marcillada rubricosa Walker.

Frons very little higher than wide. Adfrons very wide (fig. 9). Ocellus 2 about half-way between 1 and 3. Labral emargination (fig. 10) subacute, more than half deep, the basal angle very narrow. Mandible dentate, with transverse internal tooth. Spinneret obtuse at apex, parallel. Setae rather short, not distinctly raised basally. Seta III on A 8 anterior to and above level of spiracle. Prolegs of A 4 nearly as long as those of A 5, but narrower. Crochets appendiculate. Spiracle of A 7 more than half A 8. Length about 35 mm. Pale green. Pupa in thin silk in leaves. Larvae defoliate *Litsaea polyantha*.

Plecoptera reflexa Guenée.

Gardner, 1941 : 286.

Frons small, about as wide as high. Ocellus 2 distinctly closer to 1 than to 3. Labral emargination acute, more than half deep. Mandible with distal margin entire or nearly so ; internal face with a transverse ridge. Spinneret parallel sided, obtuse at apex. Setae moderate, the rings obscure, not raised ; a well-developed additional seta present lateral to the line between I and II on abdominal segments ; III on A 8 anterior to spiracle, slightly above level of its upper extremity. Prolegs of A 4 much smaller than those of A 5. Spiracles pale, narrowly oval, of A 8 about twice that of A 7. Skin microscopically granulate. Length about 32 mm. Mostly green, four fine white lines along the body. Pupa with faint bloom. Larvae defoliate *Dalbergia sissoo* and *D. latifolia*.

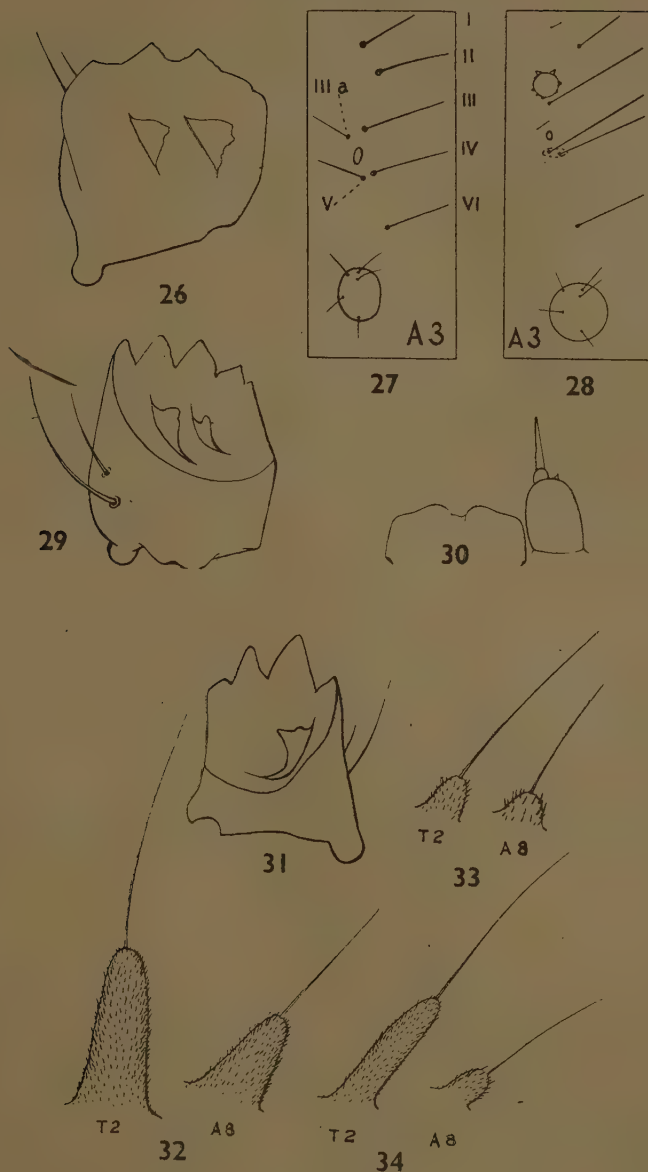
Attenda adspersa Felder.

Frons higher than wide, not much shorter than coronal suture, sides slightly sinuate. Ocellus 2 much closer to 1 than to 3. Labral emargination obtuse, about a fourth deep, the angle not curved. Mandible dentate apically, without internal tooth but the ventral margin angulate near the middle. Body setae moderately long, on small blackish plates. A 8 swollen above with two strong conical tubercles carrying setae II. Seta III on A 8 close to spiracle, anterior and above its level. Prolegs of A 4 much smaller than those of A 5. Spiracles black, of A 7 more than half that of A 8. Length about 35 mm. Head with dark lines and reticulation on a pale ground ; body greenish brown with fine white lines ; an irregular white spot laterally on A 2 and A 8 ; legs testaceous ; prolegs pale. Defoliates *Mallotus philippinensis*. Pupa with bloom ; in folded leaf.

Rhesala imparata Walker.

Gardner, 1941 : 292.

Head finely irregular above ; frons higher than wide, not much shorter than coronal suture. Ocellus 2 half-way between 1 and 3 (fig. 25). Labral emargination obtuse, about one-fourth deep. Mandible with strong distal teeth and a large internal transverse and denticulate tooth. Spinneret rather stout at base, gently tapering. Setae rather short, not raised basally ; III on A 8 is well anterior to the spiracle and nearly level with its dorsal extremity. Prolegs of A 4 not reduced, the three ventral pairs equal (or very nearly so). Spiracles pale, narrowly oval, of A 7 slightly more than half of A 8. Length about 20 mm. Head testaceous or rather darker. Body pale green with faint pale lines. Feeds on *Albizia lebbek* and *A. procera* (LEGUMINOSAE). Pupa in folded leaves ; without bloom. I can detect only two setae in VII on the first abdominal segment (instead of the normal three).



For explanation of figures see page 89.

Zethes pectinifer Hampson.

Head nearly smooth; frons moderately but distinctly higher than wide; setae well above pores. Ocellus 2 half-way between 1 and 3. Labral emargination obtuse with straight sides, nearly one-third deep. Mandible distally dentate; with large obtuse internal tooth. Spinneret moderately wide, slightly tapering, obtuse at apex. Distal segment of maxillary palp elongate. Setae rather short, the rings distinct and on small pimples; III on A 8 well anterior to spiracle and only slightly above its level. Prolegs of A 4 about as large as the other two ventral pairs. Spiracle of A 7 less than half that of A 8. Length about 20 mm. Pale green, head with lateral fuscous marks. Pupa in folded leaf. Larvae on leaves of *Adina cordifolia*.

Nyctipao crepuscularis L.

Head nearly as high as wide. Frons small, higher than wide, the setae above the level of the pores. Ocellus 2 very close to 1, distant from 3. Labral emargination subacute, rounded at base, about a third deep. Mandible without well-defined distal teeth, rather irregular; with a fairly strong internal transverse projection. Spinneret small, not much longer than wide, blunt. Penultimate segment of maxillary palp elongate, much longer than apical segment. Setae short, flush with skin at base; III on A 8 almost directly anterior to upper extremity of spiracle. Spiracles black, of A 7 more than half that of A 8. Prolegs of A 4 moderately reduced. A 8 is tumid above. Prolegs A 5, A 6 with four external and one internal setae. Length about 85 mm. Pupa without bloom; in loose silk covered with soil or in folded leaves. Larva brown speckled with black; a subdistinct oval ocellus, brown with white margin, on each side of A 1; a black dorsal intersegmental mark (broken medially) between A1 and A2. Larvae on *Smilax macrophylla*.

Pericyma umbrina Guenée.

Gardner, 1941 : 284.

Head nearly as high as wide; frons small, higher than wide. Ocellus 2 nearly touching ocellus 1, well separated from 3. Labral emargination less than a right angle, nearly half deep. Mandible without distinct distal teeth, with two small angulations near the middle; internal face with protuberant ridge. Spinneret moderately long, parallel sided, obtuse. The two distal segments of maxillary palp nearly equal in length. Setae fairly long, at most on minute pimples; III on A 8 is anterior to spiracle and well above it. Spiracle of A 7 more than half that of A 8. Prolegs of A 4 much smaller than of A 5. Length about 35 mm. A 8 not markedly tumid above. Pupa with bloom, in thin cocoon on leaves. Larvae defoliate *Acacia catechu*.

Grammodes stolidus Fabricius.

Head nearly as high as wide. Ocellus 2 almost touching 1, slightly more distant from 3. Frons higher than wide. Labral emargination an obtuse curve, rather less than a third deep. Last two segments of maxillary palp nearly equally long. Spinneret moderately long, slightly tapering to rounded apex. Mandible distinctly dentate apically and with large internal tooth. Body setae very short, not raised basally but II on A 8 on very small pimples; III on A 8 anterior to and very slightly above the upper extremity of spiracle. Spiracles black narrowly elliptical, large, of A 1 to A 7 moderately reduced. Prolegs of A 4 much smaller than of A 5. Length about 30 mm. Head with pale and dark stripes (three pale stripes on each side well defined); body with a dark band along the body above the spiracles and with numerous very fine dark lines dorsally and ventrolaterally. Legs and prolegs pale. Length about 30 mm. Larvae on *Zizyphus jujuba*, Punjab; collected by R. N. Mathur and probably correctly identified.

Calpe minuticornis Guenée.

Head distinctly wider than high. Frons higher than wide, not much shorter than coronal suture (seen in frontal view). Ocellus 2 very narrowly separated from 1. Labral emargination less than a right angle rounded at base and nearly half deep. Mandible with weak distal teeth and strong internal tooth. Apical segment of maxillary palp much shorter than preceding segment. Spinneret elongate, obtuse at apex. Labial palp with elongate basal segment. Body setae rather short and flush with the skin; III on A 8 above the level of the spiracle and far anterior. Spiracles black, of A 1 to A 7 reduced but more than half as large as that of A 8. Segment A 8 is moderately humped above. Prolegs of A 4 almost as large as those of A 5. Length about 40 mm. Head dull orange; body dull olive, each segment with two small spots (partly yellow, partly black) on each side, one dorsolateral, one ventrolateral. Legs and prolegs pale. Pupa without bloom; in loose cocoon of soil and silk. Larvae on *Cissampelos pareira* (MENISPERMACEAE).

Oraesia Guenée.

Larvae of this genus as represented by *O. rectistria* Guenée and *O. emarginata* Fabricius (Gardner, 1941 : 287, as *Calpe*) have much in common with *Calpe (minuticornis)*, but ocellus 2 is more widely separated from ocellus 1 (especially in *rectistria*, where it is almost half-way between 1 and 3); the prolegs of A 4 are much smaller than those of A 5; A 8 is convex, but not noticeably tumid above, and the coloration is very different.

O. emarginata Fabricius.

Head black, dull (except frontal area which is polished), and with four small pale spots on each side above (three in a row, one lateral). The body dull black with a dorsolateral band of yellow, white and red spots on each side; these spots are very irregular in shape and size; there is a thin line of pale spots paraventrally; a few very small pale spots elsewhere. Spiracles red with black margins except on T 1 and A 1, where they are black. Legs mostly black. Length about 45 mm. Larvae on *Cissampelos pareira*.

O. rectistria Guenée.

Similar to *emarginata* but the distal teeth of mandible sharper (in the two specimens examined); the spots in the paradorsal bands are all yellow and more transverse; the ventral rows much more distinct. Spiracles all black. Legs mostly pale. Length about 50 mm. Larvae on *Cocculus laurifolius* (MENISPERMACEAE).

Metachrostis trigona Hampson.

The final larval instar of this species differs from the preceding instar not only in having a smaller head but in the quite different form of the mandibles. I have not noticed a change of this kind in any other Noctuid, perhaps because my attention has been concentrated on mature larvae. The moth was identified by G. D. Bhasin from Hampson's description as *M. trigona* or near that.

Mature Larva. Head distinctly wider than high. Frons slightly higher than wide, not much shorter than coronal suture; the frontal setae distinctly above the level of the pores. Ocellus 2 well separated from 1 but closer to it than to 3. Labral emargination wide, obtuse but acute at the base. Mandible (fig. 12) with three acute distal teeth, the ventral one especially long and acute. Penultimate segment of maxillary palp nearly twice as long as wide and longer than distal segment. Labial palp with very long basal segment. Spinneret

elongate, reaching nearly to apex of distal seta of labial palp, slightly tapering, the apex acute; basal shield very long, acute. Body setae rather short, the setal rings inconspicuous and not raised; III on A 8 nearly directly anterior to the upper extremity of the spiracle. The three pairs of ventral prolegs equal. Spiracles pale, of A 8 narrowly elliptical and twice as large as the anterior spiracles. Body without protuberances, segments not elongate. Length about 17 mm. Pale green with no spots on head or body; sometimes crimson above on mesothorax.

Penultimate instar. Differs from the last instar particularly in the setae of the head (except the frontal pair) and setae I, II, III of the body being on very distinct small black spots and in the quite different form of the mandible. The last (fig. 13) with the distal margin entire (or at most with very feeble angulations) and with a quite strong curved subapical carina on the inner face. In addition, the penultimate segment of the maxillary palp is less elongate. Length about 19 mm. Pale green, usually with a crimson mark on T 2 above.

A batch of larvae taken from leaves of *Dalbergia latifolia* in Dehra Dun was divisible into three forms, one being at once identifiable as *Plecoptera reflexa*; the other two consisted (a) of larvae with numerous black spots on the head and body and with blunt mandibles, and (b) of larvae without black spots and with quite different mandibles, each with an acute tooth; the head of the latter form distinctly smaller than in the first form. Rearing experiments with several batches of these two forms produced only one species of moth.

Three larvae of the spotted head and blunt mandible type were isolated. These moulted (one larva dying in the process with the cast head not completely freed) and in each case the new head was without spots and the mandible sharp-toothed; the width of the head in the penultimate instar was 1.75 mm. in two cases and 1.94 mm. in one case; in all three heads of the final instar the width was 1.26 mm. It is therefore obvious that in this species the final instar differs from the previous one, especially in the form of the mandible and in having a *smaller* head. Two still smaller larvae examined (head width 1.18 mm. and 1.3 mm. respectively) are similar to the penultimate instar.

Larvae found in August–September have a pupal period of 8 or 9 days; larvae taken in October pupated in November and moths emerged 250 days later, in August of the next year. The larva of the final instar does not feed and forms its cocoon, between leaves, almost immediately. Incidentally larvae could not be found on *Dalbergia sissoo*.

Group B IVc.

(All ventral prolegs present, those of A 3 distinctly reduced.)

Key to genera or species.

- | | |
|--|---------------------------------|
| 1. Ocellus 2 about half-way between 1 and 3 | 2 |
| Ocellus 2 much closer to 1 than to 3 | 4 |
| 2. Prolegs of A 3 and A 4 minute, equal, scarcely protuberant. Labral emargination a small notch | <i>Xanthograptia trilatalis</i> |
| Prolegs of A 3 and A 4 quite distinct, protuberant. Labral emargination moderate to deep | 3 |

21. Prolegs of A 3 minute. Setae II of A 8 not at all raised . . . *Anua*
 Prolegs of A 3 small but not minute. Setae II of A 8 on feeble
 tubercles 22
22. Head and body with much blackish reticulation and speckling.
 (Internal tooth of mandible as in fig. 14) . . . *Ericcia inangulata*
 Head dull yellow green; body green with white lateral band on each
 side. (Internal tooth of mandible as in figs. 15, 16) *Sympis rufibasis*

Achaea janata L.

Gardner, 1941 : 282.

Frons small, the two setae slightly above the level of the pores. Ocelli 1 and 2 contiguous. Labral emargination on obtuse curve, nearly one-third deep. Mandible dentate, with internal tooth. Basal segment of labial palp about three times as long as wide. Spinneret rather wide, nearly parallel sided. Body setae short, not raised basally except II of A 8 on strong conical tubercles borne together on a transverse swelling; III on A 8 slightly anterior to spiracle and above its level. Prolegs of A 3 very small, of A 4 only slightly reduced. Length about 50 mm. The larva is common on *Ricinus communis* and has been recorded from numerous other plants of various families.

An immature larva of *Achaea mezentia* Stoll (length 40 mm., defoliating *Elaeodendron glaucum*, Wynaad, Madras) is very similar to *janata*, but the spiracles are black (ochreous with black rim in *janata*); the body is closely covered (except ventrally) with close fine black variegation.

Anomis Hubner.

Gardner, 1941 : 287 (*Cosmophila*, part).

Larvae of *Anomis* resemble those of *Cosmophila* (B IV a) in having an additional well-developed paradorsal seta on the anterior abdominal segments and differ in having prolegs on A 3 and in having simple (not appendiculate) crochets.

Frons higher than wide, the two setae a little above the pores. Ocellus 2 closer to 1 than to 3. Labral emargination from obtusely curved and one-third deep to more acute and nearly half deep. Mandible rather bluntly dentate; with strong internal tooth. Spinneret moderately long, broadly rounded at apex. Body setae rather short, at most on very small pimples; on small black spots. An additional well-developed seta, about half-way between II and IV on each side, is present on the first six abdominal segments; III on A 8 is anterior to and slightly above the level of, the upper extremity of the spiracle. Prolegs of A 3 strongly reduced (but not minute), of A 4 moderately reduced. Length 30-35 mm. Pupae without bloom; in loose silk cocoon between leaves or covered with soil particles.

A. fulvida Guenée (Gardner, 1941 : 288) is distinguished by the broad yellow band (subdivided by thin black lines) which runs along each side of the body above the spiracle. Labral emargination acute and nearly half deep. Larvae on *Kydia calycina* (MALVACEAE).

A. mesogona Walker (Gardner, 1941 : 289) is mostly pale green. Labral emargination rather widely curved, about a third deep. Larvae on *Rubus lasiocarpus* (ROSACEAE).

A. sabulifera Guenée (Gardner, 1941 : 288) is mostly green. Labral emargination obtuse, about one-third deep. Larvae on MALVACEAE (*Urena lobata*, *Hibiscus esculentus*, cotton).

A. figlina Butler is dark green with a fine pale line, bordered by fuscous, along the body above the spiracles. Labral emargination subacute but distinctly less than half deep. On *Grewia tiliacifolia* (TILIACEAE).

Anua Walker.

Frons rather narrow, much higher than wide and much shorter than coronal suture; the setae slightly above the pores. Ocelli 1 and 2 approximate. Labral emargination obtuse, weakly to moderately curved. Mandible moderately dentate; with prominent internal ridge. Setae rather short, not raised basally; III on A 8 anterior to upper extremity of

spiracle; VIII very short on A 1, A 2. Prolegs of A 4 strongly reduced, of A 3 minute small tubercles with crochets. Spiracles rather narrow. A 8 not tumid. Pupa without bloom; in leaves.

A. triphaenoides Walker from *Shorea robusta* was previously described (Gardner, 1941 : 283).

A. olista Swinhoe from *Quercus incana*, Garhwal, is very similar but the labral emargination is rather shallower (nearly a third deep in *triphaenoides*); colour much the same (head with close dark speckling, a solid yellow band on each side; body closely speckled).

Bamra mundata Walker.

Head very distinctly granulate. Frontal setae slightly above pores. Ocellus 2 much closer to 1 than to 3. Labral emargination nearly half deep, narrow, rounded at base. Mandible without distinct distal teeth, with strongly transverse internal carina. Labial palp with basal segment about 2.5 times as long as wide. Spinneret rather broad, nearly parallel, bilobed at the broad apex. Setae not distinctly raised basally except that A 8 has a dorsal tumidity bearing II on rounded tubercles; III of A 8 anterior to spiracle and above its level; segments A 1 and A 2 each with a paraventral pair of circles, with distinct rim and larger than normal setal rings, apparently representing setae VIII which are absent; prolegs of A 4, A 5 each with four external setae. Length about 45 mm. Dull brown-grey or green; head and body may have dark mottling; setae II, III and IV on reddish spots on most segments; spiracles dull ochreous with dark rims. Larvae on *Albizia lebbek*.

Beana terminigera Walker.

Head transverse, coarsely granulate above. Frons scarcely higher than wide, the setae above level of pores and well removed from lateral margins. Ocellus 2 very close to 1, distant from 3. Labral emargination abrupt, slightly less than a right angle and not quite half deep. Mandible with four distal teeth and two internal teeth. Spinneret slender, obtuse at apex. Body setae short, II of A 8 on distinct rounded tubercles, the others not, or scarcely, raised basally; III of A 8 nearly directly anterior to upper extremity of spiracle. Pygidium (fig. 24) with a caudad projection from middle of posterior margin; this projection obtuse at the rather narrow apex, slightly compressed. Prolegs of A 4 to A 6 subequal, of A 3 strongly reduced. Spiracles blackish, large, of A 1 to A 7 only slightly smaller than of A 8. Length about 35 mm. [Colour uncertain; the only larva (in spirit) shows some dark reticulation on head and indefinite dark markings on a paler ground on the body.] Feeds on *Ventilago calyculata*.

The pygidial "horn" is unique among Noctuid larvae examined.

Chilkasa falcata Swinhoe.

Frons higher than wide, the two setae sublateral, above level of pores. Ocellus 2 slightly nearer 3 than 1. Labrum (fig. 21) with emargination a rather wide curve, about one-fifth deep; the median setae nearer anterior margin than usual. Mandible (fig. 18) with four sharp distal teeth, the internal ribs of the two lowest teeth with one or two subapical teeth. Antenna short, the second segment less than twice as long as wide. The two distal segments of maxillary palp both elongate, nearly equally long. Spinneret extending nearly to apex of distal seta of labial palp, bilobed at apex. Body setae on small pimples; III on A 8 directly anterior to upper extremity of spiracle. Prolegs of A 4 strongly reduced, slightly larger than those of A 3, but distinctly protuberant. Body green. Length about 30 mm. Spiracles large, narrowly oval, of A 1 to A 7 moderately smaller than of A 8. Reared from an unidentified plant at a field station in Madras.

Ericeia inangulata Guenée.

Frons higher than wide, the setae above the level of the pores. Ocelli 1 and 2 approximate. Labral emargination an obtuse curve about one-fourth deep. Mandible (fig. 14)

weakly dentate distally; internal face with a strong projection bearing well-marked carinae. Spinneret rather wide, obtusely rounded apically. Body setae moderate, at most on minute pimples; III on A 8 anterior to spiracle and above its level. Prolegs of A 3 strongly, of A 4 moderately reduced. Length about 45 mm. Head with blackish reticulate markings on a pale ground, a small pale spot on each side of coronal suture; frons and adfrons paler; body closely speckled with black, rather paler dorsomedially. Pupa with faint bloom. Larvae on *Dalbergia latifolia* and *Mimosa rubicaulis* (LEGUMINOSAE).

Erygia apicalis Guenée.

The larva is peculiar in that the body is distinctly margined ventrolaterally on each side, this margin with a fringe of filamentous outgrowths (fig. 23).

Head distinctly transverse, coronal suture not much longer than frons; frontal setae well above pores. Ocelli 1 and 2 approximate. Labral emargination a weak and shallow curve. Mandible dentate, with an obtuse internal tooth. Spinneret rather wide, the apex obtusely bilobed. Body setae short, on small but distinct pimples which are slightly larger on A 8; III on A 8 above level of spiracle and more anterior. Length about 42 mm. Head grey-brown with fuscous reticulation. Body grey-brown stippled with fuscous; a black transverse band between A 1 and A 2 and between A 2 and A 3 above. Spiracles sordid white with black rims. Larvae on *Ougeinia dalbergioides*. Pupa with light bloom; in rather thick cocoon of silk with particles of debris.

On A 1 and A 2, only two setae are present in setal group VII, the third being replaced by a very distinct margined circle considerably larger than the normal setal ring.

Enmonodia vespertilio Fabricius.

Frontal setae nearly level with pores. Ocelli 1 and 2 approximate. Labral emargination subacute and rather less than half deep. Spinneret elongate, rather wide, bilobed at apex. Mandible weakly dentate, the inner face with transverse ridge. Body setae short, II on A 7, A 8 and A 9 on rounded tubercles; the anterior setae weakly raised; III on A 8 close to spiracle, anterior and slightly above its level (fig. 19). Prolegs of A 3 and A 4 distinctly smaller than the others. Length about 60 mm. Head blackish with pale mottling; medially pale; body grey-brown with black and white mottling; spiracles dull ochreous with black rims. Pupa with bloom; in leaves. Larvae on *Albizia lebbek*.

Hamodes aurantiaca Guenée.

Head very distinctly bilobed (fig. 20), wider than high; with groups of rather coarse granulation. Frontal setae rather high. Ocelli 1 and 2 approximate. Labral emargination abrupt, subacute, less than half deep. Mandible almost entire distally, feebly angulate; with a weak but distinct transverse carina on internal face. Body setae short, on small to moderate tubercles, those bearing II on A 8 the largest; III on A 8 above and anterior to the spiracle. Prolegs of A 3 rather strongly, of A 4 moderately, reduced. Length about 60 mm. Head greyish black; body grey with black, white and brown speckling; spiracles sordid white with fine black rims. Pupa with heavy bloom; in folded leaf. Larvae on *Dalbergia sissoo* and *D. latifolia*.

Haritophya biparticolor Hampson.

Head moderately transverse, wider below, moderately but distinctly bilobed above. Frons much higher than wide, not much shorter than coronal suture; frontal setae lateral and rather high above pores. Ocellus 2 approximate to 1. Labral emargination about half deep, acute. Maxillary palp with two distal segments elongate. Labial palp with basal segment about four times as long as wide. Spinneret slender, tapering distally, extending well beyond elongate second segment of labial palp. Mandible entire distally, with strong internal carina. Body setae moderate on barely distinguishable pimples which are, however, stronger on II; (pimples are more distinct in earlier instars). Seta III on A 8 almost

directly anterior to upper extremity of spiracle. Prolegs A 4 moderately, of A 3 fairly strongly reduced. Spiracles moderate; of A 7 about two-thirds that of A 8. Length 45 mm. Head brownish with black dots, with a dense black stripe on each side. Body fuscous mottled with brown. Setae black, on small white spots. Spiracles brown with black rims. Pupa without bloom; in thin silk and earth cocoon. Larvae on *Mucuna pruriens*.

Ischyja manlia Cramer.

Moore, 1884, *Lepid. Ceylon* 3: 138, pl. 163, 1b.

Frons higher than wide, the two setae a little above the pores. Ocellus 2 close to 1. Labral emargination a wide shallow curve. Mandible dentate; with strong internal tooth. Spinneret moderately elongate, broadly rounded at apex. Setae moderately long; II on abdominal segments on rounded tubercles which are large on A 1 and A 2 and less noticeable on A 8 where they are borne together on a large soft protuberance; I, on A 1 to A 3, on small pimples; III on A 8 is nearly vertically above the spiracle. Spiracles moderate. Prolegs with numerous external setae; of A 4 slightly, of A 3 moderately reduced. Length about 70 mm.

Preserved specimens have the head greyish with a black band on each side (Moore says head ochreous, dotted with black); the body with much dark speckling (Moore says varied with purplish brown and ochreous irregularly marked with short black streaks). In my specimens the second segment of the leg is blue-black. Pupa with bloom; in leaves. Larvae on *Cupania anacardioides*.

The numerous external setae on the prolegs, an unusual character outside the ACRO-NICTINAE, are very distinctive.

Lacera alope Cramer.

Ocelli 1 and 2 approximate. Frons much higher than wide, not much shorter than coronal suture; frontal setae a little above pores. Labral emargination a shallow curve. Mandible dentate with large internal tooth. Spinneret broadly rounded at apex. Setae moderate, the setal rings very distinct; II on A 8 on strong tapering tubercles, the remainder at most on minute pimples; III of A 8 anterior to spiracle and slightly above its level; V on A 1 far anterior to spiracle and not much below its level; on both A 1 and A 2 the three setae VII are distinct on each side, but seta VIII is represented by a sharply defined circular space considerably larger than the normal setal ring (fig. 17). Prolegs of A 3 and A 4 extremely small and nearly equal. Spiracles moderate, of A 1 to A 7 rather strongly reduced. Length about 50 mm. (colour in alcohol, dull brown; head brown, stippled with pale, a few clearer pale spots, frons pale; body with close stippling of black and brown dots tending to form lines; a few small pale spots above associated with setae; legs pale, prolegs dark brownish). Larvae on *Caesalpinia sepiaria* and *C. nuga* (LEGUMINOSAE). Pupa with bloom, in leaves.

Lithosiopsis torsivena Hampson.

Frons a nearly equilateral triangle. Ocellus 2 about half-way between 1 and 3. Labral emargination acute, not quite half deep. Mandible without distal teeth, with a rather weak transverse carina on internal face. Penultimate segment of maxillary palp about twice as long as wide. Labial palp with basal segment about three times as long as wide. Spinneret subparallel, broad at apex. Body setae moderate, not raised except slight pimples on posterior segments. Seta III on A 8 above and anterior to spiracle. Spiracles moderate, rather narrowly oval. Prolegs of A 4 slightly, of A 3 strongly reduced. Length about 30 mm. Colour green. Pupa in leaves. Larvae on *Milletia auriculata*.

Mecistoptera velifera Swinhoe.

Head rather strongly transverse. Frons higher than wide; setae rather above pores. Ocelli 1 and 2 approximate. Labral emargination subacute, nearly half deep, rounded at

base. Mandible with three rather blunt teeth and an internal ridge. Basal segment of labial palp about four times as long as wide. Spinneret nearly parallel, blunt apically. Body setae rather short, not raised; III on A 8 is anterior to and above the spiracle. Prolegs of A 3 very small, of A 4 larger but distinctly smaller than of A 5. Length about 30 mm. Head black with yellow speckling, with a large yellowish transverse and very irregular mark posteriorly; body blackish with several fine pale irregular lines; an orange spot behind each spiracle; two black spots above spiracles A 1 to A 4; legs and prolegs blackish. Larvae on *Aspidopterys wallichii*.

Ophiusa coronata Fabricius.

Gardner, 1941 : 284.

Head not much wider than high. Frons higher than wide, small, much shorter than coronal suture. Ocelli 1 and 2 approximate. Labral emargination subacute (slightly less than right angled) about two-fifths deep, rounded at base. Mandible with obtuse distal teeth or angulations; with large obtuse internal swelling, the surface of which has several carinae. Setae short, not raised basally except II on A 8, each on a rounded tubercle of moderate size; III on A 8 is anterior to spiracle and slightly above its level; VIII on A 1 and A 2 much shorter than the three setae of VII and in a larger setal ring. Prolegs of A 3 strongly, of A 4 moderately reduced. Spiracles large. Length about 65 mm. Head brown with sharply defined pale lines; body brown with numerous fine black lines. Pupa without bloom; in leaves. Sevastopulo (1939, *J. Bombay nat. Hist. Soc.* 40 : 689) gives colour details. Larvae on *Quisqualis indica*.

Othreis Hubner.

Frons a little higher than wide, nearly as long as coronal suture (in frontal aspect; measured "round the curve" the coronal suture is actually longer.) Ocelli 1 and 2 approximate. Labral emargination acute, rounded at the base, about two-fifths deep. Mandible with distal margin wide, three small teeth near the middle; without internal armature. Spinneret not narrowed apically. Body setae not raised basally; III on A 8 vertically above the spiracle. Segment A 8 raised into a strong transverse hump dorsally. Prolegs of A 3 strongly, of A 4 slightly reduced. Segments A 1 and A 2 each with a pair of large circular "ocelli." Larvae feed on MENISPERMACEAE. Pupae in folded leaves.

Othreis fullonia L. is described by Gardner (1941 : 290), and with special reference to colour by Moore (1881, *Trans. zool. Soc.* 11 : 64, pl. 12) and by Sevastopulo (1941, *J. Bombay nat. Hist. Soc.* 42 : 290). Mandible with part of the distal margin finely serrate. The pupa is without bloom.

Moore (*loc. cit.*) gives coloured illustrations of *ancilla* Cramer, *materna* L. and *hypermnestria* Cramer, the colour being apparently the chief specific distinction; I have seen one larva of *ancilla* which is structurally like that of *fullonia*. Moore also gives two figures of *Maenas salaminia* Cramer which, according to one figure, is very like *Othreis*; the other figure shows the four pairs of ventral prolegs equal and is probably incorrect.

Parallelia Hubner.

Prolegs of A 4 moderately, of A 3 very strongly reduced. Labral emargination acute, half or nearly half deep. Ocelli 1 and 2 approximate. Body setae at most on minute pimples except II on A 8 which are on strong conical processes. Seta III on A 8 above and anterior to spiracle. Pupae with bloom; in leaves spun together with silk. The following notes

are, in part, based on single larvae preserved in alcohol, which may not be mature. All feed on EUPHORBIACEAE.

P. crameri Moore.

Previously described (Gardner, 1946 : 291).

The general coloration is ashy grey with dark stippling tending to form bands along the body ; the frons white with a dark median line. The prolegs of A 3, although small, are not minute, the planta expanded and with numerous crochets. Larva about 55 mm. long. On *Phyllanthus emblica*.

P. arcuata Moore.

Appears to have the general coloration of *crameri* but the frons with a much larger, nearly circular, black spot ; the speckling of the body not in lines or bands. The prolegs of A 3 are minute, the planta not expanded, with six or seven crochets. Length about 45 mm. On *Glochidion* sp. ; Dehra Dun.

P. joviana Stoll.

Represented by one larva from Coorg (defoliating *Phyllanthus emblica*).

The prolegs of A 3 very small, intermediate in size between those of *crameri* and *arcuata*. The preserved larva is pale ; the head with a large black spot on each side of vertex, another on each side behind antenna, and a smaller one on each side above the adfrons ; very distinct dorsal black spots are present on A 8 and A 9 and there are indications of smaller spots on some of the anterior segments ; legs black externally ; external plates of prolegs reddish with black margins. Length 40 mm. This larva is described and figured by Moore (*Lepid. Ceylon* 3 : 175, pl. 170, fig. 9a). Head grey-white with black spots ; body bluish-grey above, yellowish beneath, with sparse black spots ; the tubercles on A 8 red.

P. amygdalis Moore.

One larva, length 30 mm., from *Phyllanthus emblica* Coorg.

Has minute prolegs on A 3 ; head mostly blackish, a small pale spot on each side near vertical sinus, a large pale lateral patch on each side and the anterior margin (including frons which has a large black mark) pale ; body pale above with dorsal lines of dark speckling ; ventrally dark ; legs pale ; prolegs dark brown ; tubercles on A 8 black.

P. algira L.

I have not seen this species, but a detailed colour description is given by Sevastopulo (1939, *J. Bombay nat. Hist. Soc.* 40 : 689). The larva feeds on *Ricinus communis* ; Calcutta.

Rhynchodontodes angulata Walker.

Frons higher than wide, setae slightly above pores. Ocellus 2 nearer to 1 than to 3. Labrum subrectangular, the emargination subacute and about a third deep. Mandible with three weak teeth and a large rectangular internal tooth. Basal segment of labial palp about five times as long as wide. Spinneret subparallel, only slightly narrowed at the apex which extends beyond second segment of labial palp. Body setae rather short, not raised ; III of A 8 anterior to spiracle and moderately above its level. Prolegs of A 4 strongly reduced, of A 3 still smaller. Length about 30 mm. Head speckled grey black, two vague pale lines on each side ; body speckled grey black with vague pale lines (one subspiracular more distinct) along the body ; without distinct black spots above. Larvae on *Indigofera pulchella*.

Speiredonia retorta L.

Head slightly wider than high. Frons higher than wide, small, much shorter than

coronal suture, the setae slightly above the pores. Labral emargination acute, rounded at base, nearly half deep. Ocelli 1 and 2 approximate. Mandible weakly dentate; with moderately protuberant internal carina. Basal segment of labial palp about four times as long as wide. Spinneret extends beyond second segment of labial palp; blunt at apex. Setae short, not raised basally: III on A 8 well above level of spiracle and anterior to it. Spiracles large. Segment A 8 not tumid above. Prolegs of A 3 strongly, of A 4 moderately reduced; prolegs of A 5 and A 6 each with four external setae. Length about 65 mm. Head blackish with pale mottling, medially pale, including adfrons and frons, the latter with a fuscous median line. Body dark brownish speckled with black and white; a lateral yellowish stripe above spiracles from T 1 to A 1 and from A 3 to A 7; setae on white spots. Spiracles sordid white with black rims. Larvae on *Albizzia lebbek* and *A. procera*. Pupa in leaves; with at most a faint bloom.

Sympis rufibasis Guenée.

Head moderately transverse. Frons higher than wide, about as long as coronal suture (in frontal view); setae very slightly above pores. Ocelli 1 and 2 approximate. Labral emargination shallow (about one-fifth deep), obtuse. Mandible as in figs. 10, 16. Spinneret rather wide, extending beyond second segment of labial palp, bilobed apically. Body setae moderate, on extremely weak pimples; III on A 8 nearly directly anterior to upper extremity of spiracle. Prolegs of A 3 strongly, of A 4 moderately reduced. Length about 40 mm. Head dull yellowish green; body dull olive green with a white subspiracular band which is continued on to the head; intersegmental skin yellow; spiracles brown with darker rims. Larvae on *Nephelium litchi*. Pupa in rolled leaves.

Thalatta Walker.

Head distinctly wider than high. Ocelli 1 and 2 approximate. Frons higher than wide, the two setae high above the pores, not far from the middle height of the frons. Labral emargination abrupt. Mandible with distal teeth and a transverse internal ridge. Body setae moderately long, on distinct pimples, those bearing II on A 8 more prominent; III on A 8 nearly directly anterior to the upper extremity of the spiracle; ventral prolegs with four external setae. Spiracle of A 8 about 1.7 times as large as that of A 7. Prolegs of A 3 much smaller than those of A 5. Larvae feed on MALPIGHIACEAE. Pupa without bloom; in folded leaves.

Thalatta fasciosa Moore.

Labral emargination more than half deep, acute, rounded at base. Prolegs of A 3 with 24, of A 4 with 29 crochets (one specimen examined). Colour (of preserved specimens) uncertain but not as dark as *precedens* and without the two bands of white spots of that, head with patches of dark brown marks on a pale ground; body probably brown with vague pale lines; a dark mark anterior to setae II on most segments; spiracles ochreous with black rims. Length 85 mm. Larvae on *Hiptage bengalensis*.

Thalatta precedens Walker.

Labral emargination abrupt but less than half deep. Prolegs of A 3 with 14, of A 4 with 25 crochets (one specimen). Head mostly black with irregular white patches; frons dark brown; body blackish with a dorsolateral band on each side, consisting of narrowly divided white and yellow spots of irregular size and shape; setae on white spots; legs and prolegs pale; spiracles black. Length about 35 mm. Larvae on *Aspidopterys wallichii*.

Xanthograptia trilatalis Walker.

Gardner, 1941 : 271.

Frons slightly higher than wide, the setae rather high above the pores. Ocellus 2 half-way between 1 and 3. Labrum only slightly wider than long, subcircular, with a small obtuse notch. Mandible feebly dentate, without internal armature. Labial palp with basal

segment only slightly longer than wide (1 : 1.3); apical seta short. Spinneret moderately wide, subparallel, extending to apex of elongate second segment of labial palp. Setae rather short, not raised basally except minute pimples posteriorly. Spiracles rather broadly oval, of A 8 a little more than twice as large as the anterior spiracles. Seta III on A 8 anterior to and nearly level with upper extremity of spiracle. Prolegs of A 3 and A 4 minute, scarcely protuberant, with seven (one specimen examined) small crochets each. Length about 20 mm. Green, the head with some fuscous mottling. On grass.

DIVISION D.

Larvae of this Division are distinguished from typical Noctuids by the fact that setal group VI is bisetose on all three thoracic segments (but a small verruca in one species of *Selepa*); in true Noctuids VI is bisetose on T 1 but unisetose on T 2 and T 3. There are no verrucae, with the one exception noted above. Prolegs are all well developed and the crochets are in a uniordinal mesoseries which may be homoideous or heteroideous. Body setae moderately long to very long.

The Division is an artificial one since the larvae of the four genera contained (*Brithys*, *Earias*, *Selepa*, *Eligma*) seem to represent three different groups with little in common. Although Hampson has included all four genera in NOCTUIDAE it is probable that only *Brithys* is a true, but anomalous, Noctuid.

In the following key are included, for comparison, certain other Noctuoid genera the larvae of which have the characters stated above.

Key to genera.

1. VI is bisetose on proleg-bearing segments (2)
 VI is unisetose on abdominal segments (3)
2. Crochets heteroideous. Only one conspicuous seta (III) above abdominal spiracles; IIIa very small. *Argina*, *Utetheisa* (ARCTIIDAE)
 Crochets homoideous. Two well-developed setae (III, IIIa) above abdominal spiracles LITHOSIIDAE (part)
3. Seta V close to IV on abdominal segments. (Ventral prolegs with four external setae) (4)
 Seta V well below the level of IV. (Ventral prolegs with three external setae) (5)
4. Crochets heteroideous. A gland above seta III on A 2 to A 7 is distinct *Selepa*
 Crochets homoideous. Without such glands *Eligma*
5. Setae II and IV of T 2 and T 3 (and usually of abdominal segments) each at the apex of a soft protuberance which may be elongate or rather short and stout. Skin densely covered with fine skin-points *Earias*
 Body setae not on soft projections (6)
6. Body setae on large shining chalazae. Spinneret short, strongly transverse *Brithys*
 Setae on small pimples. Spinneret slender *Digama* (HYPSIDAE)

Eligma narcissus Cramer.

Eligma Hubner (genotype *narcissus* Cramer) was treated by Hampson (1894, *Fauna Brit. India* 2 : 43) as an Arctiid and later (1912, *Cat. Phalaenae* 11 : 330) as a Noctuid (SARROTHRIPINAE); by Seitz (1910, Seitz, *Macrolepid.* 2 : 71) as a Hypsid and by Warren (1913 in Seitz,

Macrolepid. 3 : 291) as a Sarrothripine. More recently, according to the *Zoological Record*, 1944, *Eligma* has been transferred to the ACONTIINAE (NOCTUIDAE) by Turner (1942, *Proc. R. Soc. Qd.* 53 : 76). However, the larva of *E. narcissus* is very different from larvae of *Acontia* spp. (Gardner, 1946, *Trans. R. ent. Soc. Lond.* 96 : 67); on the other hand, it is closely related on larval characters (and incidentally on pupal characters) to *Selepa*.

Mature larva. Prolegs normal, those of A 3 to A 6 each with four external and one internal setae; crochets homoideous. Setae (fig. 27) mostly very long, on small tubercles; on abdominal segments IV is nearly directly posterior to the lower extremity of the spiracle, not more ventrad on A 7; V is close to IV and slightly antero-ventrad; IIIa rather long, anterior to upper extremity of spiracle or a little above that level; III on A 8 vertically above spiracle; VI is single on abdomen; group VII trisetose on A 1 and A 2.

Head transverse, with sharply defined granules dorsally; frons shorter than coronal suture, the two setae near the anterior margin. Labral emargination subacute, less than half deep. Ocelli 1 to 4 nearly equally spaced. Mandible (fig. 26) with two rather weak teeth near middle of distal margin and with two internal teeth. Labial palp with basal segment elongate, distal seta shorter. Spinneret rather slender, rounded at the apex which extends to near apex of second segment of palp. Body without glands (compare *Selepa*); the skin very finely granulate. Length about 40 mm.

Head mostly black, a rather broad pale line along coronal suture continues to ocelli along each side of the black frons. Body segments with a large irregular transverse black patch above; remaining surface reddish above, yellow below. Legs and prolegs pale. Spiracles oval, rather large, pale. The larva feeds on leaves of *Ailanthus excelsa* in south India and is figured by Fletcher (1914, *Some South Indian Insects* : 384).

Selepa Moore.

Prolegs normal, of A 3 to A 6 with four external and one internal setae; crochets heteroideous. Setae (fig. 28) mostly very long, on moderate tubercles but setae I and IIIa are fine, subequal and rather short: group VI is bisetose on T 2 and T 3 and unisetose on abdominal segments (but VI is a small verruca in *docilis*); IV and V in a nearly horizontal line below the spiracle, approximate; VII trisetose on A 1 and A 2. A gland-like structure above seta III on A 2 to A 7.

Head transverse with a few dorsal granules. Frons subequal to coronal suture, the two setae high above the pores. Ocelli 1 to 4 equally spaced. Labral emargination shallow, obtuse. Mandible (fig. 29) distally with three large and one small teeth and an angulation; with two separate internal teeth. Labial palp with basal segment elongate. Spinneret very much as in *Eligma*.

Selepa discigera Walker.

This species is distinguished from the other species I have seen (Gardner, 1941 : 276) by the following combination:—

VI on T 2, T 3 is bisetose (not a verruca as in *docilis*); very long ribbon-shaped setae arise from T 2, T 3, A 1 and posterior segments; the paradorsal glands large, with circular crenulated margin. The head testaceous; body spotted with black dorsally including median spots on A 2, A 8 and pygidium. Length about 20 mm. Larvae on leaves of *Terminalia tomentosa*; Coorg.

Brithys crini Fabricius.

The following notes may be added to my previous description (Gardner, 1941 : 267).

Spinneret (fig. 30) strongly transverse. Mandible distally with three sharp teeth and two

small angulations; without internal tooth. Setal group VII is bisetose on A 1, trisetose on A 2. The larvae resemble those of my Group A II (which contains HADENINAE among others) except for the bisetose VI on T 2 and T 3 and for the strong chalaze.

Earias Hubner.

Prolegs normal, equal, the ventral prolegs each with three external and one internal setae. Crochets uniordinal, homoideous. Setae moderately long, secondaries absent. Setae II and IV usually borne apically on soft projections which may be long and slender or short and rounded according to the species; these projections always conspicuous on T 2, T 3 and A 8; VI may be on smaller projections; setae I and III not raised basally. Seta III vertically above spiracle on A 8; IV higher than spiracle on A 1, lower on A 7 and A 8 and posterior on A 2 to A 6; V well below IV on A 1 to A 6; VI bisetose on thoracic segments, unisetose on abdominal segments; group VII is unisetose on A 1, bisetose on A 2; IIIa is minute and above the spiracle but anterior on A 8. The skin densely covered with minute skin points which become longer and more hair-like on the projections.

The head blackish with a transverse whitish band; with a small group of granules on each side above. Mandible distally with three teeth and an angulation. Labral emargination a shallow curve. Labial palp with basal segment elongate. Spinneret slender. Spiracles oval, black, that of A 8 not much larger than that of A 7.

Larvae feed on Malvales (MALVACEAE, BOMBACEAE) with the exception of one on *Grewia hirsuta* (TILIACEAE); buds and fruits are the usual food.

The genus was included by Hampson in the Noctuid subfamily ACONTIINAE, but is now regarded as a Hylophilid.

Key to species of *Earias*

1. Seta II on T 2, T 3 and A 8 on a rounded projection which is not distinctly longer than wide; on abdominal segments 2 to 6 seta II feebly or not raised basally (2)
 Seta II on T 2, T 3 and on most abdominal segments on elongate more or less finger-shaped projections (3)
2. Mandible without internal tooth. Second segment of antenna less than twice as long as wide *fabia*
 Mandible with small internal tooth. Second segment of antenna more than twice as long as wide near *luteolaria*
3. Mandible without internal tooth. Projections II on A 8 rather short and stout only slightly longer than wide *insulana*
 Mandible with internal tooth. Projections II on A 8 distinctly longer than wide (4)
4. Projections of setae II on T 2 and T 3 are black. Frons mostly dark, the transverse pale band of the head angulate above it *cupreoviridis*
 Projections II on T 2 and T 3 are pale. Frons pale and not breaking the regularity of the pale transverse band across the head *luteolaria*

Earias cupreoviridis Walker.

The larva was previously briefly described (Gardner, 1941 : 278).

The setiferous projections of setae II (fig. 32) are elongate on all segments from T 2 to A 9, being longest on T 2 and T 3 and shortest on A 9; of setae IV also slender, and of VI small but distinct. The frons is mostly blackish, the pale band of the head angulate above it. Mandible (fig. 31) with internal tooth. Second segment of antenna nearly twice

as long as wide. Projections II black on T 2, T 3, A 2, A 5 and A 8. Larvae on *Sida rhombifolia*; Dehra Dun.

Earias luteolaria Hampson.

The larva resembles *cupreoviridis* structurally except that the anterior projections are not quite so slender and may be distinguished by characters stated in the key. Mandible with internal tooth. Second antennal segment rather more than twice as long as wide. The frons is white and included in the transverse band of the head. Body mottled whitish, smoky laterally; projections II on T 2 and T 3 pale, orange at base, on A 2, A 5 and A 8 black, the remainder pale. Length about 18 mm. Larvae feed on flower buds of *Grewia hirsuta* (TILIACEAE); Dehra Dun.

Earias species.

Mandible with internal tooth. Second segment of antenna more than twice as long as wide. Setal projections II short and stumpy on T 2, T 3 and A 8 and represented by small tubercles on intermediate segments; IV on small tubercles. Length about 18 mm. Frons mostly pale and enclosed in the pale band of the head. Colour of body uncertain, of alcoholic specimen with little pigmentation.

Two larvae were found in fallen flowers of *Bombax malabaricum*. A reared moth superficially resembles that referred to as *luteolaria* above.

Earias fabia Stoll.

Mandible without internal tooth. Second segment of antenna distinctly less than twice as long as wide. Setiferous projections (fig. 33) of II and IV on T 2 and T 3 short, only slightly longer than wide and rounded tubercles on A 8 to A 10; setae II and IV on intermediate segments not raised basally. Length about 15 mm. The transverse white band of the head is angulate above the frons which is blackish except at the extreme apex. Pronotum partly black, an irregular pale transverse line near the middle, pygidium blackish. Body dark brown with irregular white patches (largest on A 4) above; with orange spots at bases of setae II on T 2, T 3, A 1 and at bases of IV on abdominal segments.

Preserved larvae were provided by the Government Entomologist to the United Provinces and by the Imperial Entomologist, New Delhi, from cotton and *Hibiscus esculentus* fruits.

Earias insulana Boisduval.

Mandible without internal tooth. Second segment of antenna much less than twice as long as wide. Setiferous projections (fig. 34) well developed on all segments behind prothorax, II elongate and slender on T 2, T 3 and A 1, a little smaller on A 2 to A 7, short and rounded on A 8; IV slender, elongate; V prominent on A 1 and A 2, less so on following segments. Length about 15 mm. Frons mostly white and included in the white band which is continued angulately along the coronal suture. Setiferous projections of seta II blackish on T 2, T 3 and A 2.

Larvae were provided by the Government Entomologist, Sudan, and by the Imperial Entomologist, New Delhi, from cotton, *Hibiscus esculentus* and *Abutilon* sp.; also recorded from flowers of *Althaea rosea* in Dehra Dun.

Separation of *E. fabia* and *E. insulana*.

These two species, the spotted bollworms, are serious pests of cotton in India and elsewhere. They have in common the lack of an internal tooth to the mandible and the presence of a short second antennal segment; however, *insulana*, with elongate setiferous projections on

segments from T 2 to A 7, is readily distinguishable from *fabia* with projections short on T 2 and T 3 and vestigial or absent on A 1 to A 7.

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 —, 1946, On the Larvae of the NOCTUIDAE I. *Trans. R. ent. Soc. Lond.* 96 : 61-72.
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EXPLANATION OF TEXT FIGURES 1-34.

1. *Abrostola anophioides*, 8th abdominal segment.
2. *Plusia nigrisigna*, mandible.
3. *P. nigrisigna*, spinneret and labial palp.
4. *P. nigrisigna*, labrum.
5. *Autoba angulifera*, ocelli.
6. *Hyperba aurotincta*, mandible.
7. *Calesia dasyptera*, setal map of A 8.
8. *Hiccoda dorsaroides*, labrum.
9. *Marcillada rubricosa*, head.
10. *M. rubricosa*, labrum.
11. *Cosmophila flava*, four crochets.
12. *Metachrostis trigona*, mandible of final instar.
13. *M. trigona*, mandible of penultimate instar.
14. *Ericcia inangulata*, mandible, internal face viewed slightly obliquely.
15. *Sympis rufibasis*, mandible, internal face.
16. *Sympis rufibasis*, mandible, internal face viewed obliquely.
17. *Lacera alope*, part of 1st abdominal segment, ventral view.
18. *Chilkasa falcata*, mandible, internal view.
19. *Enmonodia vespertilio*, setal map of segment A 8.
20. *Hamodes aurantiaca*, outline of dorsal margin of head.
21. *Chilkasa falcata*, labrum.
22. *Mocis frugalis*, ocelli.
23. *Erygia apicalis*, 2nd abdominal segment in lateral view, showing filamentous fringe.
24. *Beana terminigera*, dorsal view of pygidium.
25. *Rhesala imparata*, ocelli.
26. *Eligma narcissus*, mandible.
27. *E. narcissus*, setal map of A 3.
28. *Selepa discigera*, setal map of A 3.
29. *S. discigera*, mandible.
30. *Brithys crini*, spinneret and a labial palp.
31. *Earias cupreoviridis*, mandible.
32. *E. cupreoviridis*, projections bearing setae II of T 2 and A 8.
33. *E. fabia* the same.
34. *E. insulana* the same.

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THE GEOGRAPHICAL DISTRIBUTION OF THE FORMS OF THE
AFRICAN NYMPHALINE BUTTERFLIES *CHARAXES ETESIPE*
GODART AND *CH. PENRICEI* ROTHSCHILD

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WITH 2 PLATES, 7 TEXT-FIGURES AND 1 MAP.

AMONG the African *Charaxes* three species form a group characterised by having the costal margin of the underside of the hind-wing light coloured and entirely without markings. One of them (*Ch. achaemenes* Felder) has no place in this discussion, which, at first, concerns males only.

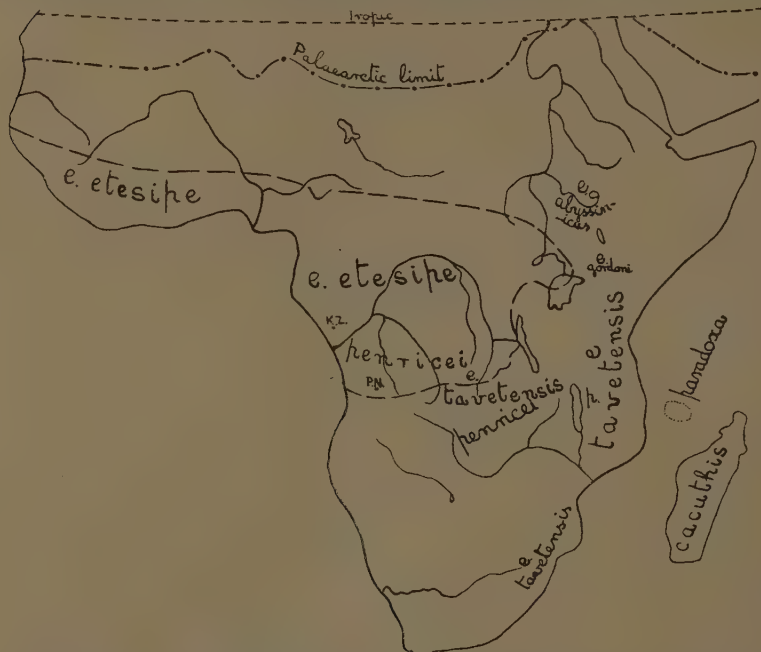
Charaxes etesipe Godart.

Rothschild and Jordan (1900) summarise the distribution of the species in all its known forms as "Tropical West and East Africa, and Madagascar." Abyssinia is included in "East Africa." *Ch. e. etesipe* Godart (Pl. 1, fig. 1) occurs from Sierra Leone to Angola and eastwards into Uganda (according to van Someren and Rogers (1929) as far as the Nandi-Lumbwa area), beyond which it is replaced by *e. tavetensis* Rothschild. Specimens in the Hope Department of the Oxford University Museum come from Bendere on the Congo-Nile divide in south Sudan, and from Lotti on the Acholi Hills along the Uganda-Sudan border. To the south *e. etesipe* is found in the south-east Belgian Congo, in the Kasai and Katanga areas. I have found no evidence that it occurs in Tanganyika Territory, except at Bukoba, just south of Uganda. *Ch. e. tavetensis* Rothschild (1894) and Rothschild and Jordan (1898) (Pl. 1, fig. 3) was described from Taveta, between Voi and Moshi in Kenya Colony. The distinctive character is the width of the blue band which is greater than in *e. etesipe* but, in at least some parts, less than in *e. cacuthis* Hewitson. Rothschild comments upon a specimen from Zomba, Nyasaland, which "has the blue post-discal patches of the fore-wing above more proximal than the other specimens, the patches being in the same position as in *cacuthis*, and the band of the hind-wing is also more proximal." This specimen will be discussed later.

The form *tavetensis* replaces *e. etesipe* in most of Kenya Colony (van Someren and Rogers, 1929) and southwards through Tanganyika Territory. A specimen in the Levick collection (now in the British Museum) bears data "Zanguebar, Nguru. Juillet 1885. R. P. Machon." I am indebted to Dr. G. Van Son for the statement that there are in the Transvaal Museum specimens from the Beira district (Zimbabwe). Lannin (1924) reports it from the Amatonga and Dondo regions in Portuguese

East Africa. A specimen at Oxford was captured in north Zululand by H. W. Bell-Marley. The British Museum (Natural History) possesses one specimen from "Nyasaland," one from Mt. Mlanje, and one from the Lualaba river, south-east Congo.

THE DISTRIBUTION OF FORMS OF *CHARAXES ETESIPE* GODART AND *PENRICEI* ROTHSCILD.



The distribution of *Ch. e. etesipe* Godart probably corresponds well with the area enclosed by the broken line --- which is Chapin's West African subregion (1932, *Bull. Amer. Mus. nat. Hist.* 65 : 90), but *Ch. e. etesipe* extends a little farther north-east of Lake Victoria, where it meets *Ch. e. tavitensis* Rothschild. It is overlapped on the south by *penricei* Rothschild, which, in Portuguese Congo at the point K.Z. (Kibokolo do Zombo) and in Angola at the point P.N. (Pungo Ndongo) has produced the form *Ch. p. dealbata* Joicey and Talbot. The distribution of *Ch. p. penricei* in turn overlaps that of *e. tavitensis* in Nyasaland and to the east of Lake Nyasa where it occurs at Songea (point p). The alternating position of the names *tavitensis* and *penricei* on the map in Rhodesia and south-eastern Congo must not be taken to indicate details of distribution, only the general occurrence in the same area.

Ch. e. abyssinicus Rothschild (1900) was described as "in the form of the band of the hind-wing intermediate between *Ch. etesipe tavitensis* and *Ch. etesipe etesipe*"; it also has the ground colour of the underside "more cinnamon." Specimens at Oxford from the mountains of south Sudan are transitional between the true Abyssinian race and *e. etesipe* (*vide table*).

Ch. e. gordonii van Someren (1936) was described from six males from the lower Meru forest, Kenya Colony, as resembling *e. tavitensis* above but with the ground colour of the underside paler, less ochreous tinged.

It is intermediate between *e. tavetensis* and *e. abyssinicus* (van Someren, *in litt.*).

Ch. e. cacuthis Hewitson (1863) (Pl. 2, fig. 5) is confined to Madagascar. It is the purport of this paper to suggest that it is more correctly placed under *penricei*. Rothschild and Jordan (1900) describe the blue band as much wider than in *e. etesipe*, and wider than in *e. tavetensis*, with, on the underside, the "white colour somewhat more extended than in the other two races." This is an important point.

Ch. e. paradoxa Lathy (1925) (Pl. 1, fig. 2) from Grand Comoro was described from thirteen males in Mme Fournier's collection, and is of considerable geographical interest. It has the white spots on the fore-wing as large as in *penricei penricei*, but the hind-wings only differ from those of *e. etesipe* by slightly larger discal blue spots. On the underside the ground colour is more yellowish and the black markings smaller. Lathy rightly points out that it resembles typical *e. etesipe* rather than *e. cacuthis* of Madagascar.

Charaxes penricei Rothschild.

The type (Pl. 2, fig. 4) was described by Rothschild (1900) from the Quebe river, Angola, and the point was made that the pale patch in area 1b of the fore-wing is more proximal than in *e. cacuthis* and that the pattern recalls that of *e. cacuthis*. The underside has "the white markings larger and purer in colour, the red bars brighter" than in *e. etesipe*. Although recorded from Angola its headquarters appear to be Nyasaland (Chintechi, and Maiwale near Fort Johnston). Five specimens in the British Museum come from the south-eastern Congo, Kikura river, and Joicey and Talbot (1922) record it from "Katanga." Lannin (1924) captured one in Rhodesia about 90 miles south-east of Bulawayo. There is a specimen in the British Museum from Tanganyika Territory, Songea. There are no records from Portuguese East Africa though Dr. G. Van Son (*in litt.*) states that its occurrence there is by no means improbable because the floristic area where it has been found in Southern Rhodesia penetrates into parts of Portuguese East Africa. Lathy (1901) figures a specimen from Zomba.

Ch. penricei peculiaris Lathy (1906) was described from a specimen from North-East Rhodesia, similar to *p. penricei* but with the blue replaced by green and, on the under surface, the darker markings heavier and the red markings not so bright. This individual was ascribed to *p. penricei* by Joicey and Talbot (1922). *Ch. penricei dealbata* Joicey and Talbot (1922, as "*penricei*") was described from two males, one from the Portuguese Congo, Kibokolo do Zombo, and one from Pungo Ndongo, Angola. It has the blue bands narrower and the white scaling reduced (Pl. 2, fig. 6).

Summarising facts of distribution we get the following:—

- | | |
|----------------------------|---|
| <i>Ch. e. etesipe</i> ... | Angola, West Africa, Uganda, Bukoba (W. coast Lake Victoria, just south of Uganda border), South Sudan, Western Kenya colony. |
| <i>Ch. e. abyssinicus</i> | Abyssinia. |
| <i>Ch. e. gordonii</i> ... | Northern Kenya Colony. |

- Ch. e. tavetensis* Eastern Kenya Colony (Taveta-Teita districts and coastal zone), Tanganyika Territory, Zanzibar, Pemba Is., Beira and Laurenço Marques, North Zululand, Nyasaland, South-eastern Congo (Lualaba river).
- Ch. e. paradoxa* Grand Comoro.
- Ch. e. cacuthis* ... Madagascar.
- Ch. p. penricei* ... Angola, Nyasaland, Songea (Tanganyika Territory), South-eastern Congo, Southern Rhodesia, North-eastern Rhodesia.
- Ch. p. dealbata* ... Angola, Portuguese Congo.

Thus *etesipe* meets *penricei* in Angola and Nyasaland; more specimens from Angola with precise data would be interesting.

The difference between these species must be discussed. Rothschild and Jordan (1900) says of *penricei* "Genital armature not essentially different from that of *Ch. etesipe*" (see text-figs. 1-7). On the other hand, the genitalia of *achaemenes* Felder do not differ materially. Thus the three members of this group of *Charaxes* do not seem separable by genitalia. The markings of the fore-wing are "similar in position to those of *etesipe cacuthis*," the patch in area 1b "more proximal than in *cacuthis*." On the underside of the hind-wing "the white markings [are] larger and purer in colour, the red bars brighter."

The general appearance of the underside of *penricei* is much brighter than in *etesipe*; in the latter there is a drab yellowish grey ground on the hind-wings, with a pattern of small white areas, and red spots bordered with black. In *penricei* the white areas are so expanded that on the basal half of the wing there is little of the drab ground colour. The white patch in area 7 distal to the basal red spots is extended in *penricei* almost, or quite, to the proximal of the paired black markings bounding a somewhat reddish band; in *etesipe* the white is well separated from the black mark by a drab area.

Similarly, on the underside of the fore-wing the same contrast holds good, especially in the basal part of area 1b which, in *etesipe*, is strongly suffused with black as far as the pale area, which is considerably contracted, so that it is only about the width of the black patch distal to it. On the other hand, in *penricei*, the pale area begins proximally on the outer side of the basal red spots and extends distally to the black patch which it meets without the intervention of the reddish border usually seen in *etesipe*. Again, in *penricei*, as Rothschild pointed out, this black patch is less obviously formed by fusion of two spots than is the case in *etesipe*. There are similar differences between the species in area 2.

Charaxes etesipe differs noticeably from *Ch. penricei* not only in the width, but also the position of the blue band on the fore-wing, as can be seen from the following table. Measurements to half a millimetre were made along vein 1 (submedian) of the fore-wing from its tip to the mid-point of the blue band (measurement A), and from the tip to the point of origin of the vein (measurement B). The position of the band is expressed by the percentage relation of A to B, the values of which are given in Table 1.

TABLE 1.

Name	No. of specimens	Type specimen	Mean value	Max. value	Min. value	Standard deviation	Standard error	Remarks
<i>Ch. e. etesipe</i>	18	—	21.84	26.4	18.9	2.02	0.48	Doctor B. M. Hobby kindly obtained the statistical values from my figures, and reported " <i>cacuthis</i> is significantly nearer to <i>penricei</i> than to <i>tavetensis</i> . The differences between the means are 7.75 and 11.11 respectively, and these differ (8.36) by more than twice the standard error (± 1.00). <i>Cacuthis</i> is the least, and <i>tavetensis</i> the most, variable." This greater variability of <i>tavetensis</i> agrees with the supposition of its more recent origin.—G. D. H. C.
<i>Ch. e. abyssinicus</i>	3	20.7	21.93	24.0	20.0	—	—	
<i>Ch. e. paradoxa</i>	2	—	24.0	24.0	24.0	—	—	
<i>Ch. e. tavetensis</i>	19	23.2	24.88	29.8	21.8	2.29	0.52	
<i>Ch. cacuthis</i>	23	36.0	35.99	38.8	34.0	1.34	0.29	
<i>Ch. p. dealbata</i>	3	40.7	36.3	40.7	32.0	—	—	
<i>Ch. p. penricei</i>	20	45.1	43.74	47.1	39.6	2.05	0.46	
<i>Ch. p. peculiaris</i>	1	44.6	44.6	—	—	—	—	
Specimen "A"	1	35.8	35.8	—	—	—	—	
Specimen "B"	1	35.7	35.7	—	—	—	—	

Further discussion of the various forms, in the light of the above table and with consideration of other features, will reveal the true relationships of the two forms of chief interest, *cacuthis* and *paradoxa*. The form *cacuthis* was described before *tavetensis* or *penricei* were known, and was placed by Rothschild in his monograph (1900) as a race of *etesipe*. He was concerned chiefly with its difference from *e. tavetensis*—e.g., in *cacuthis* the anterior portions of the blue band on the hind-wing are more closely united than in *tavetensis*, in which the spots in areas 6 and 7 are quite free from each other and 6 is cut off from 5, while in *cacuthis* there is only a distinction between spots 7 and 6, and all these are wider than in *tavetensis*. Rothschild also noted that the black border of the hind-wing was wider posteriorly in *tavetensis* than in *etesipe* and *cacuthis*, but did not compare this feature in *penricei*, in which it is much broader than in the other three.

The fact that the blue band on the fore-wing is nearer the base of the wing in *cacuthis* than in *tavetensis* escaped notice. The figures in the table show that the position of the band in *cacuthis* is significantly nearer that of *penricei* than of *tavetensis*, while it is still more different from *etesipe*.

Thus in two points on the upperside, the position of the blue band on the fore-wing and the character of the anterior part of the band of the hind-wing, *cacuthis* resembles *penricei* more than it resembles *tavetensis*.

The difference between the underside of *etesipe* and *penricei* has already been mentioned, and *tavetensis* shows the general characters of *etesipe*, of which it is undoubtedly a geographical race. It is, however, slightly transitional towards the "brighter" underside of *penricei*. But the underside of *cacuthis* shows the same brightness, and lack of the drab ground colour, as does *penricei*, so that in this also *cacuthis* is nearer to *penricei* than to *tavetensis*.

Let us now consider the most interesting race on the Comoro Isles, *paradoxa*. Reference to the table shows that it is obviously related to *tavetensis* rather than *penricei*, and the same relationship is shown in the general coloration of the hind-wing on the under surface; the drab

ground colour is more widespread than even in *tavetensis* and the white patches more contracted. Thus, just as *cacuthis* is nearer to *penricei*, *paradoxa* is nearer to *tavetensis*.

There remain *e. abyssinicus* and *p. dealbata* for further remarks. The characters of *abyssinicus* are those of a form of *etesipe*, both in position of the blue band of the fore-wing (see table) and the large amount of drab ground colour, and of black, on the underside.

The form *penricei dealbata* is the only one of all those considered which has been recorded from Portuguese Congo. It is somewhat peculiar in appearance, the band on the hind-wing being hardly wider than that of *e. abyssinicus*, although nearer to the base of the wing. Indeed, the form is not unlike two highly interesting specimens now to be discussed as "Specimen A" and "Specimen B," which seem to be *e. tavetensis*, in which the fore-wing band has been displaced towards the base of the wing. Specimen "A" is the one from Zomba which Rothschild noted, and the value for the position of the fore-wing band is 35·8 : in specimen "B" (from Chintechi, Nyasaland, in coll. Levick, now in British Museum) the value is 35·7 : these are strikingly near the mean value for *penricei dealbata* (36·3). As regards the anterior portion of the blue band on the hind-wing, the spots in areas 7, 6 and 5 in *dealbata* are free from each other : in specimen "A" only 7 and 6 are free, the band being as in normal *tavetensis*, while in specimen "B" the condition is more like that of *dealbata*, the band posteriorly being wider than in *tavetensis*, as the outer part of the cell is tinted with blue.

A point which has hitherto not been mentioned is the character of the marginal markings on the hind-wing in area 5. This part is, in *e. etesipe*, distinctly rust-red, with a linear white marking proximal to it. In *p. penricei* the rust-red is very faintly developed, and the white mark less developed than in *etesipe* : in *e. tavetensis* the rust-red is usually less developed than in *etesipe*, but the white mark is about the same. In *p. dealbata* there is no white mark, and in specimen "A" it is vestigial, in specimen "B" very small. The rust-red in *dealbata* is poorly developed as in *p. penricei* ; in "A" it is vestigial, in "B" as in other *tavetensis*.

Now in *cacuthis* it appears to be a character that the white marginal mark in area 5 is absent or at most vestigial, though the rust-red is well shown. Thus *p. dealbata* suggests that *cacuthis* is, in this respect, the degree of development of the admarginal white mark, nearer to *penricei* than to *etesipe* : the development of the rust-red is too variable in these forms for it to be of value. It may be said there that *etesipe abyssinicus* has the marginal rust-red entirely replaced by blue : this is also the case in *e. paradoxa*.

On the under surface these two abnormal specimens are equally interesting. Specimen "A" certainly belongs to the species *etesipe*, being quite like other *tavetensis*. Specimen "B", however, has the general "bright" appearance of *penricei* owing to restriction of the drab ground colour and the more reddish appearance. It has, however, in area 1b of the fore-wing, the amount of black usually shown by *tavetensis*. To sum up, specimens "A" and "B" seem to show intergrading from *e. tavetensis*

towards *penricei*, through *p. dealbata*, "B" being nearer than "A" to *penricei*.

Let us now see to what conclusion these facts lead. It is suggested that *cacuthis*, on Madagascar, is more akin to *penricei* than to *etesipe*, while *paradoxa*, on the Grand Comoro Island, belongs to *etesipe*.

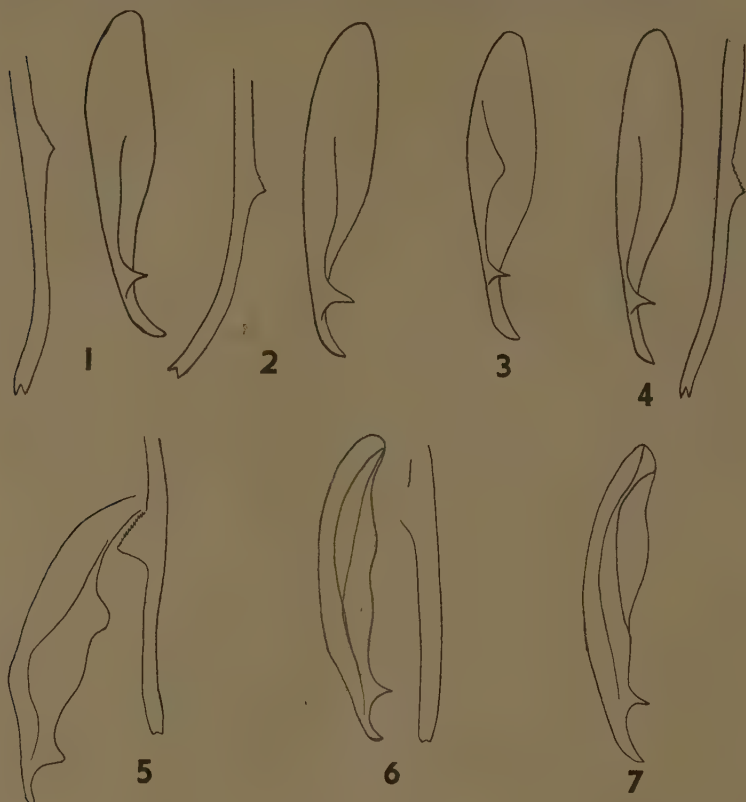
The question of the *females* of the various forms must now be considered. That of *paradoxa* presents no difficulty: it is very clearly nearer to *e. etesipe* than to *e. tavetensis*. Lathy (1925) remarked upon the fact that *paradoxa* "rassemble davantage à la race type d'Afrique occidentale . . . qu'à celle de Madagascar."

The female of *cacuthis* is peculiar, and unlike others we are considering in the strong development of yellow-brown in the pale areas of the fore-wing anterior to vein 2. Its affinity, however, with *penricei*, rather than with *etesipe*, is suggested by the rather strongly blue-edged white band on the hind-wing which approaches nearer to the base of the wing than in *etesipe*, which is also the case in *penricei*. The general tint of the white in *etesipe* females tends towards creamy white, whereas in the females now to be considered it is bluish. The difficulty is to ascertain the female of *penricei* as distinct from *tavetensis*. Rothschild described as the female of *tavetensis* two specimens from Dar-es-Salaam in the Berlin museum which are not to hand. The chief characteristic seemed to be that on the fore-wing the two white spots in area 3, and the two in area 2, are fused to make one ovate patch in each area. In females from Nyasaland, however, where males of both *penricei* and *tavetensis* occur, there is every grade of fusion or separation in these spots. In *cacuthis* there is only a faint antero-posterior line across the single patch in each area: in *paradoxa* this is more strongly defined; in *etesipe* the proximal white spot in each area is sometimes quite separate from its more distal and larger neighbour, sometimes fused almost completely. A female from Chintechi, Nyasaland, in the Hope Department, which must certainly be ascribed to *penricei*, has the areas in question well separated by an antero-posterior black bar. This is also the case in a female from the same locality in the South Kensington collection, yet in another specimen also from Chintechi the dividing bar is vestigial.

Another point mentioned by Rothschild is that the pale band on the hind-wing is, in his type of *tavetensis* female, bordered and shaded over with olive-buff. But a specimen from Pemba Island in the Tring collection which must surely be ascribed to *tavetensis* has not buff but bluish borders to the band (compare what was said above concerning a *penricei* female).

Another difficulty is created, in attempting to decide by this character, by the female form *caeruleotincta* of *e. etesipe* recently described by myself (1945).

These two specimens from Entebbe, Uganda, far removed from the haunts of *penricei*, have strongly blue-tinted and widened hind-wing bands. And if one tries to separate *etesipe* females from *penricei* females by the more creamy, or buffish, white character of their bands, one is faced with Lathy's description (1925, p. 95) of *penricei* female ab. *flavus* "caractérisée par la coloration jaunâtre des bandes et taches des deux



TEXT-FIGURES 1-7.

Genital armature (clasper and aedeagus).

Drawn from specimens in fluid mount by means of a projector. The clasper is seen from within and not flattened to the same degree in all specimens. This folding over of the edge accounts for the apparent difference in width, and for the varying appearance of the edge of a ridge running forward from the base of the tooth. There is no essential difference between them.

1. *Charaxes e. etesipe* Godart. Uganda, Jinja, R. Van Someren.
2. *Ch. e. tavetensis* Rothschild. North Zululand, Maputa, Sibangwana, H. W. Bell-Marley
3. *Ch. penricei dealbata* Joicey and Talbot. Angola, Pungo Ndongo. (The specimen figured on Plate 2, fig. 6).
4. *Ch. p. penricei* Rothschild. Nyasaland, 12 miles east of Fort Johnston, Maiwale, W. A. Lamborn.
5. *Ch. p. cacuthis* Hewitson. South-west Madagascar. (The specimen figured on Plate 2, fig. 5.)
6. *Ch. e. paradoxa* Lathy. Comoro Isles. (The specimen figured on Plate I, fig. 2.)
7. *Ch. achaemenes* Felder.

paires d'ailes, en dessus." This might be a description of the yellow banded female form *castoroides* Poulton 1926, of *e. etesipe*!

A little light is thrown upon the difficulty by comparison of a specimen from Lindi on the coast of Tanganyika Territory, and presumably out of reach of *penricei*, with the ne-allotype of *penricei* mentioned by Joicey and Talbot (1922). On the upper side no differential character can be detected, but there is a slight difference in the degree of development of the black bar dividing the white spots in the fore-wing areas 2 and 3; it is only faintly indicated in the Lindi specimen and more pronounced in the *penricei* ne-allotype, though in the latter it is less pronounced than in some specimens which are (probably) *tavetensis* with the pale spots slightly tinted with cream instead of bluish, as in the *penricei* ne-allotype. On the under surface a difference can be seen, though it is probably not adequate to distinguish between other specimens. The *penricei* female shows the paler areas much more distinctly and on the fore-wing the white patch in areas 3 and 4, leading to the margin, is larger and better defined than in the Lindi specimen. Also there is less of the drab ground colour in the *penricei* ne-allotype, it being much suffused with white.

An interesting female from Pemba Island (the only specimen known to me of either sex from that island) may be taken to be the representative of *tavetensis* seeing that an undoubted male has been taken on Zanzibar. This female is *not* yellow tinted, but has the more extended drab ground beneath, and the fore-wing spots in area 2 are fused together while in area 3 there is a trace of the dividing band.

Summing up, it is in my opinion almost impossible to say which females are *tavetensis* and which are *penricei* when taken in Nyasaland where these two overlap.

The peculiarities of distribution of these various forms call for explanation. I suggest that *e. etesipe*, so widespread through the forest region, is the older form, and that when forests were more extensive in south-east Africa than they are now it occurred also much further eastwards and may have occupied the area now given up to *e. tavetensis*. The presence in Natal, Nyasaland, Usambara, Rabai near Mombasa, and Meru (in Kenya) of forms of such a typically forest butterfly as *Pseudacraea eurytus* L. supports this. It may have been at this time that *etesipe* entered the area now separated as the Comoro Isles, and thus gave rise to *paradoxa*: apparently Madagascar was then not in continuity with the Comoros. Subsequently, recession of forests and gradual desiccation may have resulted in the adaptive evolution of *e. tavetensis* which differs from *e. etesipe* by reduction of melanin, the blue band on the hind-wing being broadened and the general tone of the underside lighter. *Penricei* is, perhaps, a step still further in that direction. It is suggested that *penricei* may at one time have extended nearer to the coastline than it seems to do now, and got across to Madagascar, though not to the Comoros, giving rise by isolation to *cauthis*.

The overlapping distribution of *e. etesipe* and *penricei* on the west (see map) and of *penricei* and *e. tavetensis* in Nyasaland, together with

the curious form *p. dealbata* in Angola and the Portuguese Congo which appears to be an intergrade, suggests that we are dealing with one of those cases of a group of forms not yet sufficiently distinct to be given specific rank. More individuals like *p. dealbata*, specimen "A" and specimen "B" might enable this point to be settled: the latter two specimens suggest the manner in which *penricei* may have come from *e. etesipe*, which is considered to be the oldest form. Many more specimens with precise data from Angola might show that *penricei* and *e. etesipe* are ecologically separated.

An endeavour should be made to obtain unequivocal females of *penricei* and *e. tavetensis* by breeding from specimens of each taken beyond the confines of the other. It has been said that no help is to be got from the male genital armature. Figs. 1 to 6 show no essential differences; the specimens being drawn unfixed in fluid were not all flattened under the cover slip to the same degree, consequently the difference in width of the clasper is merely due to the angle at which it is viewed in each case, the aspect being from the inner side. The two "horns" at the end of the clasper in both the island forms (figs. 5 and 6) seem to be slightly nearer together. The clasper in *achamenes* (fig. 7) agrees with that of *etesipe* and *penricei*.

The curious difference between the geographical relationship of the forms of the *Charaxes* on Madagascar and Comoro is strangely paralleled by *Papilio d. dardanus* Brown of West Africa and *Papilio humbloti* Oberthur of Grand Comoro, a member of the *dardanus* stock which has attained specific rank. K. Jordan (1905) pointed out that in the structure of the male genital armature *humbloti* is more like the western race *d. dardanus* than the eastern race *tibullus* Rothschild and Jordan or even the southern *cenea* Stoll, while the genitalia of *meriones* Felder of Madagascar are of eastern type. The explanation given for *Charaxes* cannot be made to apply in this case, and it is possibly a meaningless parallel.

I have searched the literature for references to the fauna of the Comoro Isles, in the endeavour to find any other cases of this kind, without success.

It is evident that in the case of the *Charaxes* that have been the subject of this paper, the representative on the Comoro Isles has found its way there at a time when Madagascar was separated from its satellite. I understand that the Comoro Isles being of igneous rock, it is difficult to determine the period when they were above the sea level. But, if I am correct in my conclusions as to the affinities of the various forms, it would seem that the Comoro Island representative (*paradoxa*) got there first, before deforestation of the east side of Africa had led to the production of *etesipe tavetensis*, and before *penricei* was formed, from which I believe *e. cacuthis* has been developed. Whether this was by means of a connection south of the Comoros, leaving them alone, or whether the ancestors of *cacuthis* were carried across the channel must for the present be left to the imagination.

Some stress is laid on the *Charaxes* because the case seems unique,

and contrary to the general harmony between the faunas of Comoro and Madagascar.

In conclusion, the following quotations will be found of interest, as showing the general agreement.

Pouillaude (1916), in his study of Madagascan CETONIIDAE, says : "Si l'on examine une carte bathymétrique de l'Océan Indien, on constate que le Canal de Mozambique est barré par une ligne de moindre profondeur, jalonnée par les Comores et unissant le nord de Madagascar à la côte africaine. Les émersions partielles ou complètes de ce seuil, par suite de régressions marines, ont permis des échanges de faunes. C'est ainsi que peut s'expliquer d'une part l'existence sur les terres aujourd'hui émergées le long du seuil, de types d'origine africaine comme le *Mausoleopsis* qui présentent des formes réparties de l'Afrique à Madagascar par les Comores et Nosy-Bé ; d'autre part la présence de genres exclusivement malgaches aux Comores aujourd'hui si largement isolées de Madagascar."

More recently, in his interesting work "La Genèse des Faunes Terrestres," Jeannel (1942) writes : "Les Comores . . . ces îles sont sans doute les restes des nappes basaltiques qui ont maintenu la jonction entre Madagascar et le continent pendant le Tertiaire et peut-être même jusqu'au Quaternaire. Leur faune et leur flore ont surtout des affinités avec Madagascar. Tous les auteurs qui ont étudié les Comores sont d'accord sur ce point. Voeltzkow d'après la faune et la flore, Fairmaire d'après les Coléoptères, notent que la grande majorité des espèces sont les mêmes qu'à Madagascar ou ont d'étroites affinités avec des formes malgaches, tandis que les types africains sont en petit nombre. Les Comores seraient donc restées rattachées à Madagascar bien plus longtemps et plus directement qu'avec le continent. . . . En réalité, la majorité des espèces doivent être des restes de la faune pliocène ou quaternaire de Madagascar."

Du Toit (1937) states that "India was still in attachment to Madagascar during mid-Cretaceous, but in the latter part of that epoch not only were marine beds being deposited on the eastern as well as on the western side of the island, but European faunal elements now made their appearance therein and on the eastern side of the Indian peninsula also, showing that water-ways had been established between the various masses. The Eocene sea in turn transgressed over the edges of East Africa and western Madagascar with minor submergences during the Miocene. The break represented by the Oligocene suggests that Madagascar became reunited to Africa temporarily. Only thus can be explained the well-established faunal relationships. . . . The north-western region of Madagascar, and with it the volcano of Great Comoro, belongs to the petrographical province of East Africa."

ACKNOWLEDGEMENTS.

I am most grateful to the Keeper of Entomology, British Museum (Natural History), for allowing me to study the specimens in his charge at South Kensington and Tring. Mr. F. Goodson has taken much trouble

in sending me data and specimens. The great kindness of Mme Fournier in sending me a pair of *paradoxa* enabled me to study more closely the central problem of this paper.

SUMMARY.

The forms of *Charaxes etesipe* Godart and *Ch. penricei* Rothschild are discussed and their distribution mapped. The fact that on Grand Comoro Island there is a representative of *etesipe*, while *cacuthis* Hewitson of Madagascar is now shown to be derived from *penricei*, suggests that their ancestors reached the islands independently when they were not connected. The distribution of *e. etesipe*, now limited to the typically West African sub-region, was possibly much more extensive, and as it receded with the forest and desiccation began, *e. etesipe* was replaced by its present eastern form *e. tavetensis* Rothschild.

The females of *penricei* and *e. tavetensis*, which occur in the same area, cannot be distinguished from each other: all these forms seem to belong to a species-complex not yet fully differentiated.

ADDENDUM.

While this article was in proof I received from Mr. T. H. E. Jackson, F.R.E.S., two females and three males which strongly support the conclusion of conspecificity. There are a female (1) from Geita, lying south of L. Victoria between Emin Pasha gulf and Mwanza Bay, Tanganyika Territory; a female (2) from Kilifi, Kenya Colony, some thirty miles north of Mombasa; a male (3) from Meru, Kenya Colony, to the north-east of Mount Kenya; a male (4) from Morogoro, Tanganyika Territory; and a male (5) from Geita.

1. This is undoubtedly a typical *penricei* female of rather small size, and the record considerably extends the known distribution of *penricei* in a very satisfactory manner.
2. This must be accepted as a female *e. tavetensis*. On the upper side it agrees with females of *e. etesipe*: the white is creamy, not bluish, and the band in fore-wing areas 1a, 1b, and 2 is more distal than in *penricei*. The cream spots in areas 4, 5, 6, 8 of the fore-wing are elongated outwards as in many, but not all, specimens of *e. etesipe*. The under surface cannot be said to be either *etesipe* or *penricei*, for I can find no difference on the underside of females which enables a distinction to be made.
3. This male is indistinguishable from *e. tavetensis* on the upper side. But on the hindwing underside in areas 5, 6, 7, the black spots representing the proximal halves of the pairs forming a chain, distal to the large white discal area, are considerably larger than in *e. tavetensis*, the spot in area 7 even blending with its outer member. This enlargement is also shown in two specimens of *e. abyssinicus* from Kaffa and Scioa in Abyssinia, in the British Museum, but in these the bistre ground colour is more developed than in the Meru specimen.

The Meru specimen was sent as an example of *e. gordonii*.

4. A specimen of *e. tavetensis*. Differs from 3 on the underside by not showing enlargement of the spots mentioned, and by being slightly darker.
5. An important specimen, from the same locality as 1, but not a typical *penricei*. It is intermediate between *e. tavetensis* and *penricei* as regards position of the blue band on the upper side of the fore-wing. It illustrates clearly a point, not previously mentioned, by which the male *penricei* clearly differs from *etesipe*. The two spots on the fore-wing in area 2, wide apart in *etesipe*, are brought nearer together in *penricei* by the displacement, towards the base, of the outer series, as shown by the measurements in area 1a. In the Geita male these spots are obviously closer together than in *etesipe tavetensis*.

The blue area on the hind-wing is broken up into separate spots, as in *tavetensis*. The underside is that of *tavetensis* with a black patch in areas 1b and 2 of the fore-wing interrupting the white discal area between the marginal black and the basal pattern.

The measurements referred to in Table 1 are, for these three males, as follows: The Meru male (3), 25.4; the Morogoro male (4), 22.6; the Geita male (5), 31.5. It is noteworthy that (5) departs towards *penricei*, the figure being higher than in any other specimen of *etesipe* examined. But it can still, on other grounds, be classed as *etesipe* rather than as *penricei*, whereas the female from the same locality is pure *penricei*.

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EXPLANATIONS OF PLATES

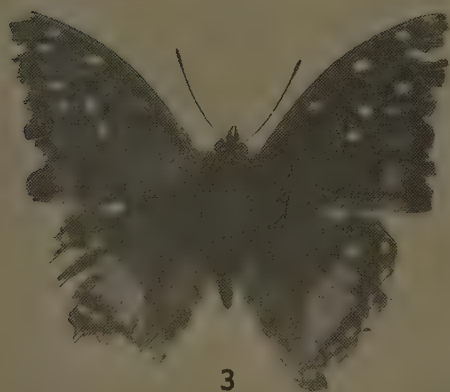
Plate I.

- FIG. 1. *Charaxes etesipe etesipe* Godart. Kenya Colony, near Kisumu, north-east of Lake Victoria, Nyangori. C. A. Wiggins, November, 1902. Oxf. Univ. Mus.
 FIG. 2. *Ch. etesipe paradoxa* Lathy. Comoro, G. F. Leigh, 28th August, 1921. Oxf. Univ. Mus., ex coll. Mme Fournier.
 FIG. 3. *Ch. etesipe tavetensis* Rothschild. Holotype. Kenya Colony, Taveta. British Museum (Nat. Hist.).

Plate II.

- FIG. 4. *Charaxes penricei* Rothschild. Holotype. Angola, Quebe river, Penrice. British Museum (Nat. Hist.).
 FIG. 5. *Ch. penricei cacuthis* Hewitson. South-west Madagascar, J. T. Last. Oxf. Univ. Mus., ex coll. H. Grose-Smith.
 FIG. 6. *Ch. penricei dealbata* Joicey and Talbot. Angola, Pungo Andongo, A. V. Homeyeri. British Museum (Nat. Hist.).

All specimens are males. Photographed by W. H. T. TAMS (figs. 3, 4); Dept. of Forestry, Oxford (figs. 2, 5); H. J. Hambidge (figs. 1, 6).



Forms of *Charaxes etesipe* Godart.



Forms of *Charaxes penricei* Rothschild.

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A NATURAL CLASSIFICATION OF LEAF-HOPPERS (JASSOIDEA, HOMOPTERA)

PART 3 : JASSIDAE.

By J. W. EVANS, M.A., D.Sc.
(*Imperial Institute of Entomology.*)

Manuscript received 24th October, 1946.
(Read 5th February, 1947.)

WITH 36 TEXT-FIGURES.

In the first part of this series (Evans, 1946*a*) the super-family JASSOIDEA was divided into five families, and in the second part (1946*b*) accounts were given of the families AETALIONIDAE, HYLICIDAE and EURYMELIDAE. It is not my intention to discuss the MEMBRACIDAE, hence only one family, the JASSIDAE, remains.

McAtee (1934) was of the opinion that the leaf-hoppers of the world are so numerous and varyingly differentiated that any given character can be found in almost any condition of development somewhere among them, and that to try and segregate these insects into well-marked families seemed a hopeless task, since attempts to draw sharp lines of distinction fail in every direction. This opinion will be, to some extent, shared by all who have any knowledge of the jassid fauna of the world and not merely of a restricted area. Nevertheless, none will at the same time deny the existence of several distinct groups of leaf-hoppers, even though it is often difficult to differentiate between these by means of characters based on persistent structural features. Because of the lack of such features the preparation of a key to the sub-families and tribes of the JASSIDAE has not been easy and the key presented on page 114 is admittedly imperfect. The illustrations have been carefully selected to demonstrate the principal characteristics of each natural group, and it is hoped that these will compensate for the shortcomings of the key.

The genera listed include all those recorded in, and previous to, volume 82 of the *Zoological Record* (1945). Every effort has been made to examine as many genotypes as possible, and in instances where genotypes have not been available I have determined the position of genera by referring to published figures and descriptions. Descriptions alone are often misleading and even good figures are sometimes inadequate, hence it is inevitable that some genera will have been incorrectly placed.

Those groups of leaf-hoppers which display no clear evidence of close relationship with other groups are recognised as sub-families, while well defined groups, which can be associated with others on the basis of presumed close genetic affinity, are classed as tribes. Of necessity the various corresponding divisions are of unequal status, but this is unavoidable.

SUB-FAMILIES AND TRIBES OF THE JASSIDAE.

Division Ulopides.		Division Macropsides.	
ULOPINAE		MACROPSINAE	
Ulopiini	(fig. 1)	Macropsini	(fig. 18)
Megophthalmini	(fig. 2)	Nioniini	(fig. 19)
Cephalelini	(fig. 3)	AGALLINAE	(fig. 20)
LEDRIINAE		AUSTROAGALLOIDINAE	(fig. 21)
Ledriini	(fig. 4)	MELICHARELLINAE	(fig. 22)
Stenocotini	(fig. 5)	IDIOCEBINAE	(fig. 23)
Koebeliini	(fig. 6)	COELIDIINAE	(fig. 24)
Thymbrini	(fig. 7)	NEOCOELIDIINAE	(fig. 25)
HECALINAE		TYPHLOCYBINAE	(fig. 26)
Hecalini	(fig. 8)	TARTESSINAE	(fig. 27)
Dorycephalini	(fig. 9)	JASSINAE	
Eupellicini	(fig. 10)	Penthimiini	(fig. 28)
Paradorydiini	(fig. 11)	Krisnini	(fig. 29)
APHRODINAE		Gypnini	(fig. 30)
Aphrodini	(fig. 12)	Selenocephalini	(fig. 31)
Ernomenellini	(fig. 13)	Jassini	(fig. 32)
Evacanthini	(fig. 14)	Trocnadini	(fig. 33)
Signoretini	(fig. 15)	Reuterellini	(fig. 34)
TETTIGELLINAE		EUSCELINAE	
Tettigellini	(fig. 16a-e, j, k)	Euscelini	(fig. 35a-f, j, k, 36a-c)
Proconiini	(fig. 16h, i, l-o, s)	Platymetopiini	(fig. 36d-p)
Mileewanini	(fig. 16c, d, f)	Xestocephalini	(fig. 35g-t)
Makilingiini	(fig. 16p-r)	Balcluthini	(fig. 36q-t)
NIRVANINAE	(fig. 17)	Macrostelini	(fig. 36u-x)

DISTRIBUTION OF THE JASSIDAE.

The JASSIDAE probably occur wherever plant growth is to be found. The oldest known, undoubted representative of the family is *Mesojassoides gigantea* Oman (1937) from the Cretaceous of Colorado. Such earlier fossils as have been ascribed to the JASSIDAE (e.g., *Triassojassus proavittus* Tillyard, 1919, from the Upper Triassic of Queensland), while in some instances referable to the super-family Jassoidea, are not representatives of the family JASSIDAE. Nevertheless, it is possible that true Jassids did occur as early as Triassic times.

In the table which follows, the time during which jassids have developed and spread is divided into four periods. No attempt is made to associate these periods with particular geological epochs, as to do so would be unjustified, since our knowledge of the present distribution of these insects is incomplete.

The various groups have been allotted to their positions on the basis of a balance between the factors of evolutionary level, as determined by structural development, habits and food-plants, and of their present geographical distribution. The table, as well as serving to bring together information concerned with the occurrence of the family as a whole, serves to separate relict faunas from those of more recent distribution.

I have assumed that the distribution of the Euscelini, which is universal, has taken place comparatively recently. This raises the problem as to why, if the Euscelini have been enabled to spread all over the world, possibly in late Tertiary times, older groups have a more restricted distribution. The answer is probably to be sought in the plasticity of leaf-hoppers in this tribe, which has enabled them to survive, and become adapted to, a wide range of environmental conditions. Further, their association with grasses may offer an added

explanation, since these plants, as well as being of almost universal occurrence and wide adaptability, are capable of spreading with great rapidity.

Period	Present Universal Distribution	Present Restricted Distribution
1	Ulopini ¹	Cephalellini (S. Africa, Australia, New Zealand).
2	Ledrini, Hecalini, Paradorydiini, ¹ Macropsini, IDIOCERINAE, TYPHLOCYBINAE, Jassini,	Megophthalmini (Europe, E. Africa and W.N. America). Koebellini (W.N. America). Stenocotini (Australia).
3	Aphrodini, ² Evacanthini, ² Tettigellini, AGALLINAE, ² COELIDIINAE, ² Penthiini, ² Selenocephalini, ² Platymetopiini, ² Xestocephalini. ²	Thymbrini (Australia, New Zealand). Errhomenellini (Europe, N. America). Dorycephalini (Russia, N. America). Eupeliciini (Europe, N. Africa). Signoretini (Tropical Africa, Oriental Region). Mileewanini (S. and Tropical Africa, Oriental Region). Krisnini (S. and Tropical Africa, Oriental Region, Costa Rica). NIRVANIINAE (S. and Tropical Africa, Oriental Region, Australia, Costa Rica). Nioniini (N. and S. America, Oriental Region). Proconiini (N. and S. America, Oriental Region). NEOCOELIDIINAE (N. and S. America). Gyponini (N. and S. America). TARTESSINAE (Australia, Oriental Region). MELICHARELLINAE (N. Africa, Turkestan, N. India). Makilingiini (Philippines). AUSTROGALLOIDINAE (Australia). Trocnadini (Australia). Reuterellini (Australia).
4	Euscelini, Macrostelini, Balcluthini	

¹ Not recorded from N. and S. America.

² Either absent from Australia or else limited to Queensland.

³ Not recorded from Europe.

Size, Coloration and General Appearance.

Jassids range in size from a length of 2 mm. to a length of 30 mm. While in general the tendency has been for evolutionary development to be accompanied by increasing size, some of the smallest leaf-hoppers belong to the most recently developed groups. The predominant colour of the more primitive groups, as well as the most usual colour throughout the whole group, is brown. This is followed by green, and then by orange, yellow, red, black and white. Some forms have a simple, but vivid, colour pattern, others an intricate pattern design.

The most usual shape of a jassid is that of a narrow wedge, but there is considerable departure from this type, frequently associated with an abnormal cephalic development. Striking changes in the shape of the pronotum also occur, but are unusual, and they are associated particularly with the Ledrini and the Macropsini.

A few jassids resemble insects belonging to other Orders; thus *Lissocarta vespiformis* Fabricius, from British Guiana, is remarkably similar to a brown and yellow wasp in appearance, while *Doda laudata* Distant, from Malaya, which is black and has reduced wings, suggests a fly. Some resemble plant spines and seeds (*Cephalelus* spp. and *Paradorydium* spp.) and several are protectively coloured. The majority depend for their safety, not so much on protective coloration as on their power of taking a sudden leap when danger threatens.

Feeding Habits.

The most primitive jassids feed on moss and reeds and live at the bases of woody plants. A few (e.g., *Eupteryx filicum* Newman) feed on ferns, but this habit is more probably a recent than an ancient association. Leaf-hoppers occupying a middle position in the evolutionary scale are largely arboreal, while those of most recent development feed on grasses and herbaceous plants, though not limited to these plants.

While many species are restricted to a single host, others have a wide range of food-plants and a few feed equally on trees, shrubs and grasses. Also, while breeding may be confined to a single plant-species, or to a limited number of plants, adult insects may be less restricted in their feeding habits, and in some instances different generations breed on different plants.

Most leaf-hoppers are phloem feeders, but the TYPHLOCYBINAE, with the exception of *Empoasca fabae* Harris, feed on the mesophyll of leaves. Putnam (1941) has pointed out that the fact that none of the TYPHLOCYBINAE are involved in virus transmission can be correlated with this habit.⁴

Although all leaf-hoppers are essentially plant-feeders, several have been recorded as sucking blood on occasion (Lawson, 1920; China, 1929; Myers, 1929). Myers states that this habit only takes place under unnatural conditions, and that most of the attacks recorded have occurred after the insects have been attracted by a bright light. The same author mentions an instance of a leaf-hopper (*Erythroneura mori* Matsumura) feeding on caterpillars and thereby causing the development of black patches.

Life-history and Habits.

The eggs are inserted into plant tissue and may be partially or, as is more usual, completely embedded. When partially embedded they are usually covered by secretions left by the ovipositing female. Sometimes they are laid singly, sometimes in groups, and they may occur both in soft and in woody tissue and even in the cracks of dead wood.

⁴ At least three *Empoasca* spp. have been recorded as virus vectors.

The winter is passed in various ways, the more usual being in the egg-stage. Large numbers of leaf-hoppers hibernate in the adult stage and in a few instances the nymphs overwinter.

Attendance by ants, which is of general occurrence among the AETALIONIDAE, EURYMELIDAE and MEMBRACIDAE is unusual among the JASSIDAE. De Bergevin (1910) has recorded the attendance of ants on *Macropsis nana* H.S. in North Africa, and Chatterjee (1934) mentions that ants feed on the sugary excretion of *Petaloccephala nigrilinea* Walker in India.

The nymphs of the majority of forms share with the adults the power of leaping into the air when disturbed. While feeding they tend to remain immobile, and Scrivener (1931) has recorded a nymph of *Gypona octolineata* Say as having remained in the same position for a period of three weeks.

Description and Discussion of Jassid Structure.

Head. In Part 1, a concept of a primitive jassid head was presented. Such a head had the ante- and post-clypeus forming a single sclerite⁵ (fig. 18*d*); the antennae lying in front of, or in line with, the anterior corners of the eyes, overhung by prominent ledges (Fig. 18*a, d*); the frons entirely ventral in position, separated from the post-clypeus by a transverse epistomal suture, and bounded laterally by frontal and posteriorly by postfrontal sutures (fig. 27*a, b*); the lora⁶ extending posteriorly as far as the anterior tentorial pits, which are situated at the inner corners of the antennal depressions (figs. 4*f*, 18*a*); a transverse suture (indicative of the position of the original anterior margins of the sides of the head) defining the posterior limits of the maxillary plates (figs. 1*a, b, 4g*); and the ocelli, ventral in position, and lying close to the junction of the frontal and postfrontal sutures (figs. 6*a, 23a*).

While there exist at the present time no jassids which retain a combination of all these primitive features, yet in two groups forms occur which retain a large, though a different, selection of them. These groups are the Ulopini (fig. 1) and the Macropsini (fig. 18), and I suggest that each of these groups lies close to the base of two separate lines of jassid development.

Although the Ulopini usually retain maxillary sutures, and have the frons, which may be separated from the post-clypeus by a vestigial epistomal suture, ventral in position (except in *Coloborrhis*, fig. 1*i, j*), they are specialised in other respects. Thus the antennae have migrated posteriorly, accompanying the posterior development of the post-clypeus, while the ocelli either lie in marginal depressions and are separated from the face by a transverse ridge, or they are on the crown of the head.

⁵ The absence of a suture separating the ante- from the post-clypeus may also be due to secondary loss.

⁶ In Part 1 I made the suggestion that the lora were of clypeal origin, though at the same time I accepted the possibility that they might have been derived from part of the paraclypeus. I am now of the opinion that they have been derived from the ventral portion of the paraclypeal lobes and that the condition, which occurs in the nymphs of the PELORIDAE, in which the lora are fused with the clypeus posteriorly, is a secondary development.

In the Macropsini, the backward extension of the post-clypeus has not been accompanied by a corresponding movement of the antennae and the antennal ledges, and these have remained nearer to the anterior than to the posterior corners of the eyes. In consequence, the lora have not been stretched, and as a result they have not lost their posterior and original points of contact, but they are still associated with the tentorial pits and the inner corners of the antennal depressions. The frons, and the ocelli likewise, have retained their primitive position, but the maxillary sutures have been lost.

From such types of heads as those of the Ulopini and the Macropsini there have been many and varied developments, and these will be discussed in later sections. As, however, jassid classification depends to a great extent on the correct interpretation of head structure, and in particular on the recognition of the limits of the frons, it will be appropriate at this point to pay some attention to this sclerite.

The reason why the recognition of the frons is important will be apparent if fig. 8*d* is compared with fig. 22*a*. In both figures there are present three median cephalic sclerites :—anteriorly the reduced labrum, followed by the narrow rectangular ante-clypeus, posterior to which is a large plate bearing muscle impressions and having the antennae lying close to its lateral margins. A superficial examination of these heads would suggest that the large sclerites in each of the two insects figured are structurally identical, and the fact that in fig. 8*d* the ocelli are close to the eyes and marginal in position might not appear of special significance.

I have stated earlier that the primitive position of the ocelli is close to the posterior apices of the frontal sutures, and though there are instances in which the ocelli are no longer in this position, they are exceptional. In both of the figures referred to the ocelli are in their primitive position, as will be appreciated if fig. 8*d* is compared with fig. 8*a*. However, the suture forming the posterior margin of the large central sclerite in fig. 8*d* is the epistomal suture, that is the suture which limits the frons anteriorly, while in fig. 22*a* it is the postfrontal suture. In other words, while in one head the frons is incorporated in the median sclerite, in the other it lies posterior to it, and is in fact largely on the crown.

The frons in its original condition was a rectangular facial sclerite bounded anteriorly by the epistomal suture, laterally by the frontal sutures and posteriorly by the postfrontal sutures (fig. 29*a*). In insects with biting mouth parts, the epistomal suture is a thickened fold which lies between the anterior mandibular articulations. In the Homoptera there is no need for a brace in this position and in most jassids the epistomal suture is vestigial or absent. In consequence the frons seldom retains its separate identity, but is usually amalgamated with the post-clypeus. Further, the dilator cibarial muscles, which originally were attached only to the inner surface of the post-clypeus, have tended to migrate posteriorly and to be attached also to the frons (fig. 29*a*).

The epistomal suture, which is always facial in position, occurs in

the following illustrations : figs. 1a, h, d, 3a, 4a, d, 5a, d, 6a, 7a, 8a, d, as well as in several later figures.

The frontal sutures, which extend posteriorly from the lateral apices of the epistomal suture as far as the ocelli, may be entirely ventral in position (figs. 5a, 6a, 8a, 10a, 11a, 23a, 25a) or in part on the face and in part on the crown (figs. 4a, 12a, b, 16j, k).

The postfrontal sutures, which extend from the anterior apex of the coronal suture as far as the ocelli, may be facial in position (fig. 18a) or on the crown (fig. 12b).

None of these sutures are completely stable ; thus the epistomal suture may be absent (figs. 1b, 19a) ; the frontal sutures may be absent (fig. 4c, d, g) or the postfrontal sutures absent (figs. 4h, k, 8b, 23f).

Thorax. In most leaf-hoppers the pronotum is wide laterally and the propleurae separate the eyes from the bases of the tegmina (fig. 1g). However, in several groups a tendency exists for the propleurae to narrow, so that the eyes come to lie close to the bases of the tegmina (fig. 22b). In only two groups, the Ledrini and the Macropsini, does the pronotum sometimes depart appreciably from its usual shape. In the Ledrini it may bear raised vertical flanges or be produced laterally (fig. 4m). In the Macropsini it is often steeply declivous and sometimes humped, and its most extreme development is illustrated in fig. 18d.

Legs. The typical jassid hind tibia is long and somewhat flattened, and bears four rows of spines, one row along each edge. In most instances the spines along one edge are stronger than those in the other rows and are mounted on prominent bases (fig. 4t). A hind tibia such as the one in the illustration referred to, which is adapted for jumping purposes, has been derived from one which is short and quadrilateral in section and which bears a few small hair-like spines (fig. 1k). The shape and armature of the hind tibiae in general supply characters of but limited value for taxonomic purposes, although sometimes they furnish a useful guide for indicating relationships.

Tegmina. The nature of the venation of the tegmen served in Part 1 to separate the various jassoid families from each other. A tegmen with typical jassid venation is illustrated in fig. 1l. In several groups the venation is reduced to a varying extent (figs. 17l, 25j, l) ; there may be additional cross-veins, especially between R and the costal margin (fig. 17k) or the venation may be reticulate (fig. 22d). In only one group, the Stenocotini, does the venation sometimes depart from the basic pattern to a significant extent. In the Stenocotini, the tegmen, as well as having subsidiary costal veinlets and the two anal veins fused apically to form a Y-vein, has also a first cubitus with more than two branches. On the basis of the character of tegminal venation alone, grounds might seem to exist for removing the genera comprised in the Stenocotini from the rest of the JASSIDAE, and for giving this tribe family status. However, other features disclose that a close relationship exists between the Stenocotini and more than one undoubted jassid group, which suggests that this departure of the venational pattern from the normal,

a departure which even within the Stenocotini is not universal, is a secondary development.

Several leaf-hoppers are brachypterous, and in a few instances, where wings are absent, and hence the insects incapable of flight, the tegmina have become thickened and elytra-like.

When considered by itself, the character of tegminal venation is seldom of much assistance in deciding the position of a jassid, but as a subsidiary character, used in conjunction with others, it often proves of great value.

Wings. A typical jassid wing was illustrated in Part 1 (fig. 14). Apart from instances of reduction due to the fusion of adjacent veins, or to the loss of veins (figs. 26*h*, *i*, 32*l*), there is no significant departure from the basic type, except in the Signoretini (fig. 15*f*) and in the TARTESSINAE (fig. 27*f*), in both of which groups the marginal vein continues on to the anal area.

Male Genitalia. I have already suggested, in Part 2, that a condition in which the aedeagus is in direct contact with both the anal segment and the basal plate is probably ancestral to one in which the aedeagus is in contact with either the basal plate or the anal segment. In the AETALIONIDAE the aedeagus retains both attachments; likewise in the Ulopini (fig. 1*m*) and the Cepheleini (fig. 3*d*). In the EURYMELIDAE the ventral association with the basal plate has been lost, while in all the JASSIDAE, apart from the ULOPINAE, the ventral contact is retained and the dorsal one lost, and the segmental membrane, which separates the ninth from the tenth segment, serves to support the aedeagus dorsally.

In many jassids the sternite of the ninth segment occurs as a separate sclerite (fig. 5*f*); in others it is fused with the tergite (fig. 4*s*). There may be no development of a pygophore (fig. 3*d*); the pygophores may be wide and simple (fig. 21*f*) or they may be wide and bear spines or accessory clasping processes (figs. 5*f*, 14*d*, 19*h*).

While for specific identification, and for help in the determination of the limits of a genus, the structure of the male genitalia furnish invaluable guides, they would not seem to be of great significance, except in a few instances, for the recognition of the higher categories.

Discussion of Head-structure in relation to classification.

I have already suggested that the Ulopini and the Macropsini lie close to the base of two separate lines of jassid descent, and on page 106 the various sub-families and tribes which I propose to recognise are listed in accordance with this concept. To those jassids which may well have been derived from the same stem as the Ulopini I am giving the group name Ulopides, and the other group I am calling the Macropsides. The inter-relationships between the various tribes and sub-families in each division will be discussed in the appropriate sections. Here I propose merely to indicate certain significant features of the head structure of representatives of each division, in order that the basis of my system of classification may be more readily understood.

Ulopides (figs. 1-17).

The leaf-hoppers in this division may be divided into six groups on the basis of characters furnished by the structure of the head:—

- (i) Forms in which the frons is ventral and the ocelli remain in their primitive facial position (figs. 2*d*, 6*a*).
- (ii) Forms in which the frons is ventral, and the ocelli are in marginal depressions, or are separated from the face by a transverse ridge (figs. 1*b*, 2*a*, 5*a*, *d*, *c*, 7*e*).
- (iii) Forms in which the frons is ventral and the ocelli are on the crown (fig. 1*d*, *e*).
- (iv) Forms in which the posterior apices of the frontal sutures terminate at the margin between the face and the crown, but the frons itself lies partly on the crown (figs. 8*a*, 11*a*).
- (v) Forms in which the frontal sutures extend on to the crown (figs. 4*h*, 12*b*, 16*k*).
- (vi) Forms in which the ocelli lie in marginal depressions and all trace of the ventral portion of the frons is lost, due to the posterior encroachment of the post-clypeus (figs. 14*a*, 15*a*, *b*).

If the figures referred to are examined, it will be found that in some instances the various groups do not correspond with recognised divisions. This feature serves to emphasise the difficulty attending jassid classification, as the characters outlined above were selected as the best available for the purpose of segregating related units. It does, however, demonstrate the close inter-relationship existing between the various tribes of the Ulopides, even though, apart from the position of the antennae, they have not a single stable character in common. ✓

In order to appreciate how the frons, which was originally a part of the face of the head, can come to lie on the crown, it must be assumed that the jassid head was originally evenly rounded and did not consist of a separate face and a crown. Following the posterior extension of the post-clypeus, accompanied by the backward migration of the antennae, the antennal ledges and the anterior arms of the tentorium, the frons will have come to lie posterior to the eyes, instead of between them. When the head was then flexed into two or more planes, a development which has occurred independently in several groups, a part of the frons would assume a dorsal position. An increase in size of the frons often results from the production of the head, because such an increase almost invariably takes place anterior to the coronal suture (fig. 17*g*), although it may also take place between the hind margin of the head and the apex of the coronal suture (fig. 17*n*).

Macropsides (figs. 18-36).

The heads illustrated in figs. 18-24 all exhibit a feature in common, which is that, even though the separate identity of the frons may be lost and the fronto-clypeus extend as far as the hind margin of the face, the antennae and the antennal ledges remain close to the anterior corners of the eyes. Associated with this feature are the presence of both the frons and the ocelli on the face of the head.

In fig. 25 a new development is apparent, and a comparison of *a*, *c* and *e* will explain one method by which the antennal ledges may be displaced, accompanied by a corresponding change in the position of the ocelli.

In figs. 28-34 illustrations are given of a group of leaf-hoppers of diverse appearance, though of common descent, in which the antennae have secondarily assumed a posterior position. They share an interesting character, which may be lost in the more specialised forms; this is the apparent overlapping of the antennal ledges on to the post-clypeus (figs. 28*a*, 30*a*). The real significance of this character will be appreciated if figs. 1 and 2 in Part I are referred to, where the antennal ledges are shown as the lateral continuations of the epistomal suture. Although in insects in this group of genera the frons was originally ventral in position (fig. 29*a*), it has come, in part, or in whole, to lie on the crown, due to the flexing and subsequent flattening of the head (fig. 28). In some instances it has become squeezed against the hind margin of the face, without extending on to the crown, even though the ocelli have become dorsal in position (fig. 30).

How the frons may come to lie in part on the crown is again illustrated in figs. 35 and 36, which represent a group of genera with vestigial antennal ledges.

It is probable that no other single family of insects occurs in which is to be found such great diversity in the shape and structure of the head. The reasons why the JASSIDAE have developed such a variety of head-shapes may well be, as suggested in Part I, associated with the loss of contact which has occurred between the anterior and the posterior arms of the tentorium. In the MEMBRACIDAE, in which likewise the two sets of arms are separate, the head conforms to a comparatively stable pattern. This may be, because in this family the head usually lacks a crown, due to the abnormal development of the pronotum. In those membracid genera in which the pronotum is of normal proportions (e.g., *Endoiastus* Osborn) a crown is sometimes developed and the head in consequence differs widely from the usual membracid type.

Key to the Tribes, and to such Sub-families as are not divided into Tribes, of the JASSIDAE.

- | | |
|--|---------------------|
| 1. Antennae closer to the anterior than to the posterior corners of the eyes; if nearest to the posterior corners, then the antennal ledges extending on to the post-clypeus; ocelli seldom on the crown | 22 |
| Antennae closer to the posterior than to the anterior corners of the eyes; ocelli usually on the crown | 2 |
| 2. Ocelli on the face of the head, not sunk in depressions | |
| | Koebeliini (fig. 6) |
| Ocelli marginal, sometimes in depressions, or on the crown | 3 |
| 3. Ocelli marginal, not in depressions, or on the crown, close to the anterior border | 9 |
| Ocelli in marginal depressions, or on the crown distant from the anterior border | 4 |
| 4. Ocelli in marginal depressions | 13 |
| Ocelli on the crown | 5 |

5. Fronto-clypeus considerably swollen, the muscle impressions visible in dorsal aspect 16
 - Fronto-clypeus not considerably swollen, or if swollen, then the muscle impressions not visible in dorsal aspect 6
6. Antennae exceptionally long, or the head spatulate or shovel-shaped 18
 - Antennae short or of moderate length; head neither spatulate nor shovel-shaped 7
7. Maxillary sutures usually distinct; antennal ledges roundly arched; labium very long 15
 - Maxillary sutures vestigial or absent; antennal ledges not roundly arched 8
8. Venation of tegmen complete; ante-clypeus apically re-curved; principal mounted spines on the hind tibiae decreasing in size from the apex to the base Thymbrini (fig. 7)
 - Tegmina often short, venation seldom complete; ante-clypeus not re-curved apically; hind tibiae lacking prominent spurs 9
9. Antennal ledges prominent; ante-clypeus exceptionally large Errhomenellini (fig. 13)
 - Antennal ledges weak or vestigial; ante-clypeus of normal size Aphrodini (fig. 12)
10. Crown produced, arrow-shaped; crown and pronotum usually carinate 11
 - Head not arrow-shaped, sometimes spatulate; neither the crown nor the pronotum carinate Hecalini (fig. 8)
11. Head foliaceous, ocelli on the crown Eupelicini (fig. 10)
 - Head not foliaceous, ocelli marginal 12
12. Head and pronotum with short white hairs, not punctate Dorycephalini (fig. 9)
 - Head and pronotum lacking short white hairs, usually punctate Paradorydiini (fig. 11)
13. Frons entirely on the face; head not carinate 15
 - Frons in part, or entirely, on the crown; head carinate 14
14. Tegmen with cross-vein r present Signoretini (fig. 15)
 - Tegmen with cross-vein r absent Evacanthini (fig. 14)
15. Tegmen with a Y-vein in the clavus Stenocotini (fig. 5)
 - Tegmen with the anal veins separate for their entire length 20
16. Tegmen with a reduced clavus, a wide appendix and lacking vein M_{1+2} Mileewanini (fig. 16c, d, f)
 - Tegmen with a clavus of normal proportions, a narrow appendix and with vein M_{1+2} present 17
17. Antennal ledges thickened, widely overlapping the post-clypeus; anterior tibiae apically dilated or quadrilateral in section and with a groove along the exterior surface Proconiini (fig. 16h, i, l-o, s)
 - Antennal ledges obscure, not widely overlapping the post-clypeus; anterior tibiae rounded Tettigellini (fig. 16a-e, j, k)
18. Antennae unusually long, labium very short NIRVANINAE (fig. 17)
 - Antennae short or of moderate length 19
19. Face not emarginate beneath the eyes; lora exceptionally small Makilingiini (fig. 16, p-r)
 - Face emarginate beneath the eyes; lora of normal proportions Ledrini (fig. 4)

20. Maxillary plates of moderate width, maxillary sutures vestigial or absent Megophthalmiini (fig. 2)
 Maxillary plates narrow, maxillary sutures usually distinct 21
21. Head narrowly triangular in shape Cephalini (fig. 3)
 Head not narrowly triangular in shape Ulopiini (fig. 1)
22. Antennal ledges vestigial, the face never wider than long, nor the head spatulate 38
 Antennal ledges distinct; if indistinct or absent, then the face wider than long, or the head spatulate or the tegmen with a wide appendix 23
23. Eyes of normal proportions; antennal ledges overlapping the fronto-clypeus, or the margin between the face and the crown acute, with the ocelli marginal or on the crown 32
 If the antennal ledges overlap the fronto-clypeus, then the eyes unusually large; otherwise not as above 24
24. Venation of the tegmen reticulate MELICHARELLINAE (fig. 22)
 Venation of the tegmen not reticulate 25
25. Appendix of the tegmen usually narrow 28
 Appendix of the tegmen wide 26
26. Wing with the marginal vein extending on to the anal area; pronotum heart-shaped TARTESSINAE (fig. 27)
 Wing with the marginal vein not extending on to the anal area; pronotum not heart-shaped 27
27. Tegmen with vein M_{1+2} always present; hind tibia short with an armature of weak spines IDIOCERINAE (fig. 23)
 Tegmen with vein M_{1+2} usually absent; hind tibia with an armature of dense spines COELIDIINAE (fig. 24)
28. Antennae exceptionally long; venation of the tegmen often reduced and indistinct NEOCOELIDIINAE (fig. 25)
 Antennae short; venation of the tegmen complete 29
29. Eyes unusually large, but not prominent; head in three transverse planes AUSTRORAGALLOIDINAE (fig. 21)
 Eyes of normal proportions, often prominent 30
30. Pronotum small, neither declivous nor strongly arched anteriorly AGALLINAE (fig. 20)
 Pronotum large, arched anteriorly and often declivous or humped 31
31. Maxillary plates narrow; lora often swollen Macropsini (fig. 18)
 Maxillary plates of moderate width; lora not swollen Nioniini (fig. 19)
32. Wing with vein R_{4+5} fused apically with vein M_{1+2} 36
 Wing with these veins separate for their entire length 33
33. Ocelli situated on a narrow marginal rim which separates the crown from the face; antennal ledges prominent SELENOCEPHALINI (fig. 31)
 Ocelli situated either on the face or on the crown, and if lying on a narrow marginal rim, then the antennal ledges vestigial or absent 34
34. Ocelli on the crown, which may be either flat or convex; antennal ledges distinct Gyponiini (fig. 30)
 Ocelli on the face, close to its hind margin but if on a well-differentiated crown, then the antennal ledges vestigial or absent 35
35. Ocelli on the face, close to its hind margin; crown sharply differentiated from the face KRISININI (fig. 29)
 Head variable in shape; ocelli on the face and marginal in position, or on the crown Penthimiini (fig. 28)

36. Head flattened and the crown extensive ; ocelli marginal Reuterellini (fig. 34)
 Head not flattened ; a crown, if developed, narrow 37
37. The pronotum and the head steeply declivous, forming one curved surface as far as the antennal ledges Trocnadini (fig. 33)
 The pronotum not steeply declivous ; the head with or without a crown Jassini (fig. 32)
38. Tegmen with reduced venation, frequently lacking an appendix and usually with an oval wax cell in the costal region TYPHLOCYBINAЕ (fig. 26)
 Tegmen usually with complete venation, but if the venation is reduced, then the appendix is wide and a wax cell is lacking 39
39. Venation of the tegmen usually reduced 42
 Venation of the tegmen complete 40
40. Eyes exceptionally small ; pronotum wide laterally Xestocephalini (fig. 35*g-i*)
 Eyes of normal size 41
41. Face of the head not emarginate beneath the eyes ; antennae long ; tegmen with veins R_{1a} and R_{1b} usually reflexed Platymetopiini (fig. 36*d-p*)
 Face of the head emarginate beneath the eyes ; antennae short ; tegmen with veins R_{1a} and R_{1b} seldom reflexed Euscelini (fig. 35*a-f, j, k*)
 Tegmen long and narrow Balcluthini (fig. 35*q-i*)
 Tegmen of normal proportions Macrostelini (fig. 35*u-x*)

Ulopides.

The six sub-families comprised in this division of the JASSIDAE fall into three natural groups. One group comprises the ULOPINAЕ, LEDRINAЕ and HECALINAЕ, another the APHRODINAЕ and the TETTIGELLINAЕ, and the third group consists solely of the NIRVANINAЕ.

The first of these groups cannot be defined within circumscribed limits. It includes both very large and very small leaf-hoppers, which are predominantly brown in colour, although several species are green. Pattern development and the occurrence of other colours does occur, but is restricted, and the head, thorax and tegmina, either entirely or the clavus only, may be pitted. The head is usually narrowly produced in front of the eyes, or it may be arrow-shaped or spatulate. In the more primitive forms the maxillary sutures are retained and the lora maintain their association with the tentorial pits (being linked with the pits by either a ridge or a vestigial suture). The post-clypeus is never considerably swollen, and in those instances in which it encroaches on to the frontal region, it usually only occupies a narrow central portion of the frons (fig. 8*a*).₁

ULOPINAЕ.

The ULOPINAЕ comprise small leaf-hoppers, brown in colour, with numerous pits on the head, thorax and tegmina and sometimes with sparse short white hairs. The labium is long, the maxillary suture (fig. 1*a, ms*) sometimes distinct, the antennal ledges curved and usually closer to the posterior than to the anterior corners of the eyes, the

antennal depressions deep and the eyes prominent. The veins of the tegmina are sometimes raised in relief and sometimes the venation is obscure, and the tegmina may be elytra-like or reduced to small pads, and wings may be absent.

The sub-family comprises three closely related tribes, the Ulopini, Megophthalmiini and Cephalini.

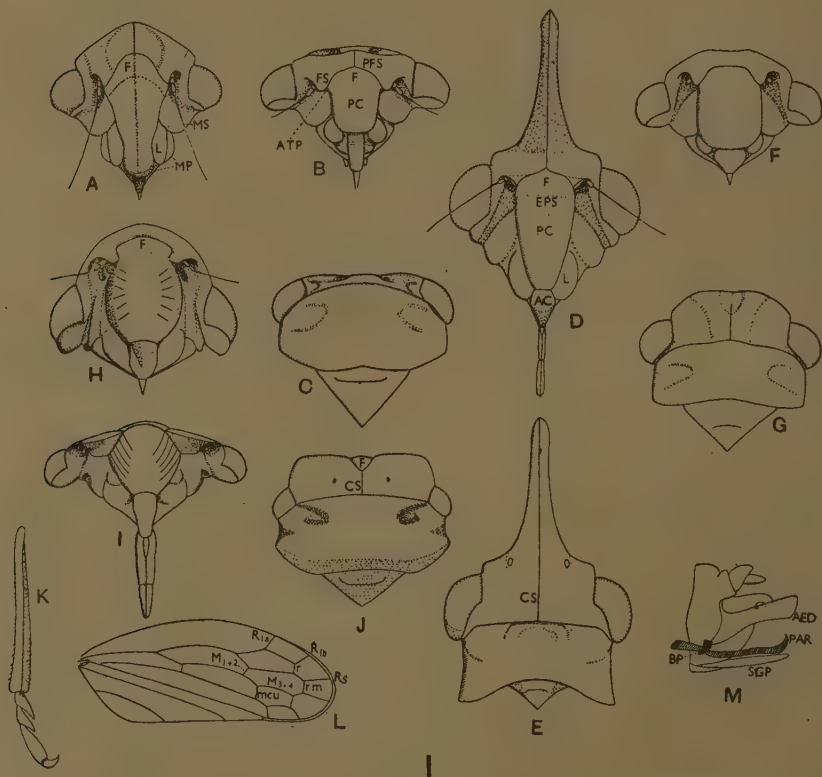


FIG. 1.

A, *Austrolpa brunensis* Ev., head; B, *Moonia variabilis* Dist., head; C, *M. variabilis*, head and thorax, dorsal aspect; D, *Uloprora risdonensis* Ev., head; E, *U. risdonensis*, head and thorax, dorsal aspect; F, *Ulopa reticulata* F., head; G, *U. reticulata*, head and thorax, dorsal aspect; H, *Caplopa turneri* Ev., head; I, *Coloborrhis corticina* Germ., head; J, *C. corticina*, head and thorax, dorsal aspect; K, *Austrolpa kingensis* Ev., hind tibia and tarsus; L, *Moonia variabilis*, tegmen; M, *Austrolpa kingensis*, male genitalia.

Ulopini (fig. 1).

Distribution.

Universal, with the exception of the Nearctic and Neotropical zones.

Size, Coloration and General Appearance.

In size, the Ulopini range from 2.5 to 5 mm. in length, and in colour they are various shades of brown, sometimes with white markings on the tegmina. The head, thorax and tegmina are rugose, or pitted with deep, sometimes glistening pits, and may have a sparse covering of short white hairs. The tegmina may be elytra- or pad-like and hind wings either present or absent.

Food-plants and Habits.

Ulopa reticulata Fabricius and *U. trivialis* Germar occur in Europe at the roots of heather and low-growing plants respectively (Douglas, 1875; Edwards, 1896). *Moonia albimaculata* Distant has been recorded from *Santalum album*, *Webera corymbosa*, *Dodonea viscosa* and *Pterocarpus indicus* in India (Pruthi, 1934); *Coloborrhhis* sp. from *Brachystegia randii* in Rhodesia and from *Bauhinia* in Sierra Leone; *Taslopa* spp. from reeds growing in damp places, *Austrolpa* spp. from grass tussocks, and *Uloprora risdonensis* Evans from the base of low shrubs, in Tasmania. *Ulopella terminicola* Poisson, from West Africa, has been recorded as occurring in a termite mound (Poisson, 1938).

In general, representatives of this tribe are slow-moving, inactive insects, incapable of jumping and often also incapable of flight, and apart from species in the genera *Moonia* and *Coloborrhhis*, they would all seem to live in concealed situations.

Description.

Head. The labium is long with two visible segments, and the ante-clypeus is long and narrow, or bulbous and pear-shaped, and is separated from the post-clypeus by a distinct transverse suture. The lora are large and swollen, and may extend as far as, or beyond, the outer margins of the maxillary plates. The maxillary plates are narrow and maxillary sutures are usually retained. The post-clypeus, which may overhang and partially conceal the ante-clypeus, is sometimes swollen, either entirely or anteriorly only. A distinct frons is sometimes retained and is usually on the face of the head, although in forms in which the head is flexed across the axis of the antennal ledges, the frons may assume a dorsal position. Frontal and postfrontal sutures are always present. The antennal ledges are curved and may terminate medially as lobe-like processes. The antennal depressions are deep, and continue anteriorly as channel-like depressions, which extend as far as the anterior margin of the head in the neighbourhood of the eyes. The ocelli are either in marginal depressions or on the crown, and sometimes lie close together on either side of the coronal suture; they may also be widely separated and lie either close to the anterior margin of the crown or nearer to the posterior than to the anterior margin. They may be well developed, rudimentary, or absent, and the eyes are prominent, often bulbous.

Thorax. The pronotum is wide laterally, sometimes collar-like, and may have narrow lateral paranota; it is usually antero-laterally depressed and may be declivous. The propisterna are not concealed by the head. The scutellum usually has a deep transverse slit and the katapisterna of the mesothorax are produced as a pair of finger-like processes.

Legs. The tibia may be quadrilateral in section or widely flattened, and the hind tibiae short, with only a few hair-like spines, or long, with a fringe of hair-like spines.

Tegmina. The tegmina may be fully developed or elytra-like, and hence functionless, or they may be reduced to short, flat pads. The veins are raised in relief and the venation may be of the complete normal jassid pattern, reticulate to a varying degree, or obscure.

Wings. The wings may be fully developed and have normal jassid venation, or lack the anterior branch of the radius, or they may be absent.

Male Genitalia. The base of the aedeagus usually extends between the anal segment and the basal plate; the parameres are long and the ninth segment retains its separate identity.

Genera comprised in the Ulopini.

Austrolpa Evans.

1937, *Pap. Roy. Soc. Tasm.* 1936 : 47.

Type—*Austrolpa brunensis* Evans (Tasmania).

Bobacella Kuznetsov.

1929, *Rev. Russe. Ent.* 23 : 271.

Type—*Bobacella teratocera* Kuznetsov (South Russia).

Bohemia Stål (new name for *Euryprosopum* Stål (praeocc.), a synonym of *Coloborrhis* Germar).

1855, *Öfvers. Vetens-Akad. Förh. Stockh.* 1855 : 97.

Caplopa Evans.

1947, *Trans. R. ent. Soc. Lond.* 98 : 252.

Type—*Caplopa turneri* Evans (South Africa).

Coloborrhis Germar.

1836, *Silb. Rev. Ent.* 4 : 72.

Type—*Coloborrhis corticina* Germar (South Africa).

Conchyotettix Oshanin (*nomen nudum*).

1891, *Tapiski Imp. Russ. geogr. Obschtoch.* 23 : 45, 67.

Type—*Conchyotettix tianschanicus* Oshanin (*nomen nudum*).

Daimachus Distant.

1916, *Faun. Brit. Ind. Rhyn.* 6 : 225.

Type—*Daimachus exemplificatus* Distant (South India).

Euryprosopum Stål (see *Bohemia* Stål).

1853, *Öfvers. Vetens-Akad. Förh. Stockh.* 1853 : 267.

Type—*Euryprosopum sobrina* Stål (Natal).

Gubela Distant (synonym of *Coloborrhis* Germar).

1910, *Ins. Transvaal.* 10 : 232.

Type—*Gubela bellicosa* Distant (Transvaal).

Kahavalu Kirkaldy.

1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 371.

Type—*Kahavalu gemma* Kirkaldy (New South Wales).

Megulopa Lindberg.

1924—*Notulae Ent.* 4 : 106.

Type—*Megulopa sahlbergorum* Lindberg (Egypt).

Mesargus Melichar.

1903, *Homopt. Faun. Ceylon* : 175.

Type—*Mesargus asperatus* Melichar (Ceylon).

Mesoparopia Matsumara.

1912, *Annot. Zool. Japon.* 8 : 27.

Type—*Mesoparopia nitobei* Matsumara (Formosa).

Moonia Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 197.

Type—*Moonia sancita* Distant (North India).

Oclasma Melichar (synonym of *Coloborrhis* Germar).

1905, *Wien. ent. Zeit.* 24 : 293.

Type—*Oclasma degenerata* Melichar (East Africa).

Ozias Jacobi.

1912, *Ergebn. Deutsch. Zentr. Afrik. Exp.* 4 : 40.

Type—*Ozias pedestris* Jacobi (East Africa).

Radhades Distant.1912, *Ann. Mag. nat. Hist.* (8) 10 : 606.Type—*Radhades crassus* Distant (Tenasserim).*Sichaea* Stål.1866, *Hemipt. Africana* 4 : 106.Type—*Acocephalus misellus* Stål (South Africa).*Sitades* Distant.1912, *Ann. Mag. Nat. Hist.* (8) 10 : 608.Type—*Sitades fasciatus* Distant (Bengal).*Taslopa* Evans.1942, *Pap. Roy. Soc. Tasm.* 1941 : 29.Type—*Taslopa montana* Evans (Tasmania).*Ulopa* Fallen.1814, *Spec. nov. Hemipt. disp. Meth. Exp.* : 19.Type—*Ulopa reticulata* Fabricius, 1794 (Scandinavia).*Ulopella* Poisson.1938, *Bull. Soc. ent. Fr.* 43 : 13.Type—*Ulopella terminicola* Poisson (West Africa).*Uloprora* Evans.1939, *Trans. Roy. Soc. S. Aust.* 63 : 44.Type—*Uloprora risdonensis* Evans (Tasmania).

Taxonomic Notes.

The genera comprised in the Ulopini have been variously placed in the past, and in many instances their true inter-relationships have not been appreciated. Fieber (1875), Van Duzee (1892), Melichar (1896), Ribaut (1936) and Ossiannilsson (1946) all recognised a family, the ULOPIDAE, of status equivalent to the JASSIDAE, CERCOPIDAE and CICADIDAE. Signoret (1879) divided the "Jassides" into five groups, of which the "Ulopides," characterised by lacking ocelli, were one. Kirkaldy (1906) referred the ULOPINAE to the MEMBRACIDAE, and Haupt (1929) referred them to the AETHALIONIDAE. Oshanin (1912) recognised the ULOPINAE as a sub-family of the JASSIDAE, while Baker (1923) and Evans (1939*b*) recognised the group as a family, the ULOPIDAE, comprised in the Jassoidea.

Mesargus was placed in the Acocephalini by Melichar, *Daimachus* in the LEDRINAE by Distant, and Kirkaldy created a sub-family, the KAHAVALUINAE, for the reception of *Kahavalu*. Although Stål (1866) referred *Ulopa* to the JASSIDAE, he considered *Coloborrhis* to be a Membracid, the latter genus being placed in the AETHALIONINAE by Goding (1931), and in the LEDRINAE by Naudé (1926) and Haupt (1929). Distant placed *Moonia* in the BYTHOSCOPINAE, a position which was accepted by Pruthi (1934), although Baker (1923) had earlier drawn attention to the close relationship between this genus and *Ulopa*.

Bobacella is only tentatively included in the Ulopini; the genotype, which was found in a marmot's nest, was referred to a new tribe, the Bobacellini, by Kuznetsov, because of the unusual shape of the antennae.

It is probable that several Ulopids have been incorrectly ascribed to genera comprised in other jassid groups, as has, for instance, *Ledra truncatiformis* Walker, 1857, from Singapore. Van Duzee in 1892

described a *Ulopa canadensis* from Canada, which was found in moss, and though his description certainly suggests a leaf-hopper belonging to the Ulopini, in his catalogue (1917) this species is listed as a synonym of *Agallia quadripunctata* Provancher.

Megophthalmini (fig. 2).

Distribution.

Europe, East Africa, and Western North America.

Size, Coloration and General Appearance.

The Megophthalmini range from 3 to 5 mm. in length, and in colour they are various shades of brown. The head, thorax and tegmina may be pitted.

Food-plants and Habits.

Megophthalmus scanicus Fallen occurs at the base of grasses, and feeds on the surface roots of low-growing plants.

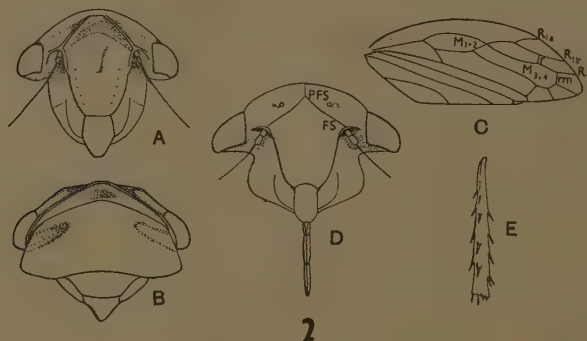


FIG. 2.

A, *Megophthalmus scabripennis* Edwards, head; B, *M. scabripennis*, head and thorax dorsal aspect; C, *M. scabripennis*, tegmen; D, *Brenda arborea* Ball, head; E, *B. arborea*, hind tibia.

Description.

Head. The labium, of which the basal segment may be exposed, is long, and the anteclypeus is separated from the post-clypeus by a transverse suture. The lora are narrow and not inflated and do not extend laterally as far as the margins of the maxillary plates. The maxillary plates are of moderate width and, while vestiges may remain of the maxillary sutures, these are never so well defined as in the Ulopini. The post-clypeus may be flat or convex, and the frons, with which it forms a continuous sclerite, may be flat or concave, and is always ventral in position. Frontal and postfrontal sutures are present, or replaced by carinae, and the antennal ledges are curved, and the antennal depressions deep. Ocelli may be present or absent; when present they may be situated on the face or on the crown, except in species with foliaceous carinae, in which they lie in depressions between the hind margin of the face and the frontal ridges. The eyes are prominent, but not globose.

Thorax. The pronotum, which is narrower laterally than in the Ulopini, has similar lateral depressions and the pro-episterna are only partially concealed by the head. The scutellum has a deep transverse slit, but the katapisterna of the mesothorax are not produced into finger-like processes.

Legs. The tibiae are quadrilateral in section, and the hind tibiae are armed with a few short, strong spines.

Tegmina. The venation may be normal and complete, or reticulate, and the veins are usually raised in relief.

Wings. The wings may be fully developed or absent.

Genera comprised in the Megophthalmini.

Brenda Oman.

1941, *J. Wash. Acad. Sci.* **31** : 205.

Type—*Paropulopa arborea* Ball (California).

Megophthalmus Curtis.

1833, *Ent. Mag.* **1** : 193 (Jan.).

Type—*Megophthalmus bipunctatus* Curtis (England).

Odomas Jacobi.

1912, *Ergebn. Deutsch. Zent. Afrik. Exp.* **4** : 32.

Type—*Odomas myops* Jacobi (Ruenzori).

Paropia Germar (synonym of *Megophthalmus* Curtis).

1833, *Silb. Rev. Ent.* **1** : 181 (Aug.).

Type—*Ulopa scanica* Fallen (Europe).

Paropulopa Fieber.

1866, *Verh. zool. bot. Ges. Wien.* **1866** : 500.

Type—*Paropulopa lineata* Fieber (Pyrenees).

Tiaja Oman.

1941, *J. Wash. Acad. Sci.* **31** : 207.

Type—*Paropulopa californica* Ball (California).

Taxonomic Notes.

Fieber (1875), followed by Melichar (1896), recognised a family, the PAROPIDAE, equivalent to the JASSIDAE and the CERCOPIDAE, while Signoret (1879) considered the "Paropides," characterised by having the ocelli on the anterior margin of the head, as one of the five families of the "Jassides." Kirkaldy (1906), Oshanin (1912), Haupt (1929), De Long and Caldwell (1937) and Oman (1943) considered the MEGOPHTHALMINAE (or PAROPIINAE) as a sub-family of the JASSIDAE, while Baker (1923) and Evans (1939*b*) recognised the PAROPIIDAE as a family of the JASSIDAE.

While there has thus been agreement as to the need for the recognition of a separate group to contain *Megophthalmus* and related genera, there has been less unanimity in the selection of the "related genera." Thus Baker (1923) asserts that Stål correctly placed *Signoretia* in the MEGOPHTHALMINAE and claims affinity between *Ulopa*, *Paropia* and *Stenocotis*. Haupt divided the PAROPIINAE into two tribes, the Paropiini and the Adelungini, the former including *Paropia*, *Koebelia* and *Stenocotis*, and the latter *Adelungia*; De Long and Caldwell also placed *Koebelia* in the PAROPIINAE.

Of these various associated genera, *Ulopa* is certainly close to *Megophthalmus*, and *Stenocotis* and *Koebelia* have certain features which

denote a common ancestry, but neither *Signoretia* nor *Adelungia* are correctly placed, even though species in the former genus are pitted on the head and thorax, and those in the latter have the ocelli similarly placed to species comprised in the genus *Brenda*.

Cephalelini (fig. 3).

Distribution.

South Africa, Australia and New Zealand.⁷

Size, Coloration and General Appearance.

The Cephalelini are small, narrow leaf-hoppers, which range from 5 to 12 mm. in length. They are brown in colour, and the head, thorax and tegmina are punctate with shallower pits than in the Ulopini. A few species have short, thick white hairs on the head and thorax and several, which in appearance resemble plant spines or seeds, have very long heads.

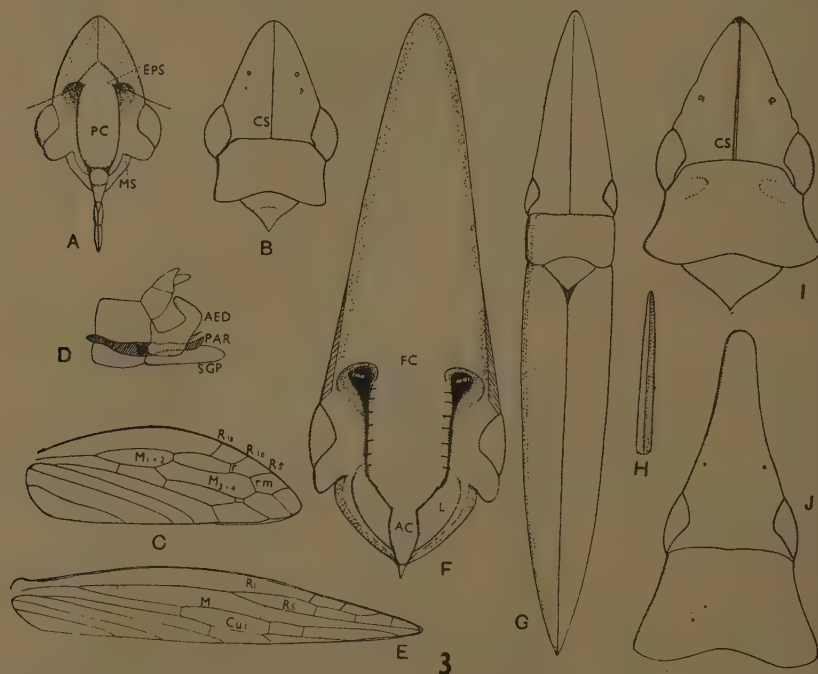


FIG. 3.

A, *Anacephaleus carribensis* Ev., head; B, *A. carribensis*, head and thorax, dorsal aspect; C, *A. carribensis*, tegmen; D, *Anacephaleus latus* Ev., male genitalia; E, *Cephalelus leptocarpus* Myers, tegmen; F, *C. leptocarpus*, head; G, *C. leptocarpus*; H, *Paracephaleus montanus* Ev., hind tibia; I, *Anacephaleus latus*, head and thorax, dorsal aspect; J, *Paracephaleus montanus*, head and pronotum, dorsal aspect.

⁷ It is probable that they occur also in Chile, as the RESTIONACEAE, to which they are apparently confined, grow also in Chile.

Food-plants and Habits

Cephalelus infumatus Percheron has been recorded from the rush, *Dovea tectorum*, in South Africa (Naudé, 1926); *C. hudsoni* Myers and *C. leptocarpi* Myers from the rush, *Leptocarpus simplex*, in New Zealand (Myers, 1923), and *Paracephaleus montanus* Evans from the rush, *Restio australis*, in Tasmania. The Cephalelini are unable to jump and the majority are also incapable of flight.

Description.

Head. The labium is long, and the ante-clypeus, which narrows anteriorly, is separated from the post-clypeus by a deep groove or an ill-defined suture. The lora do not extend as far as the outer margins of the maxillary plates and the maxillary plates are narrow. The sides of the post-clypeus are approximately parallel, and although the frons cannot be identified with certainty, it is probably entirely ventral in position. The head, posterior to the antennae, is convex in short-headed, and concave in long-headed species. The antennal ledges are curved, sometimes to such an extent that the antennae become inwardly directed, and the antennal depressions are deep and continue anteriorly as grooves lying on either side of the post-clypeus. Ocelli may be present or absent, and when present occur always on the crown. The eyes, which are prominent in short-headed species, are in line with the sides of the head in those forms which have produced heads.

Thorax. The pronotum may be dorsally flat and collar-like, or declivous, and wider posteriorly than anteriorly, and it may be depressed antero-laterally; the pro-episterna are partially exposed. The scutellum may have a deep transverse cleft and the katepisterna of the mesothorax are produced posteriorly as finger-like processes.

Legs. The tibiae are either quadrilateral in section or considerably flattened, and the hind tibia are short, with a few hair-like spines.

Tegmina. The tegmina may have complete or reticulate venation, and the veins may be raised in relief, or the venation obscure. In fig. 3c, M_3 and M_4 are shown apically as separate veins, but this is an unusual development.

Wings. Wings are usually absent, and when present, as in *Paracephaleus montanus*, they have a reduced venation.

Male Genitalia. The base of the aedeagus extends between the anal segment and the basal plate, the parameres are long, and the ninth sternite has lost its separate identity.

*Genera comprised in the Cephalelini.**Anacephaleus* Evans.

1937, *Pap. Roy. Soc. Tasm.* 1936 : 43.

Type—*Anacephaleus minutus* Evans (Western Australia).

Cephaleleus Percheron.

1832, *Mag. Zool.* 9 : 48.

Type—*Cephalelus infumatus* Percheron (locality unknown).

Dorydium Burmeister, 1835 (synonym of *Cephalelus* Percheron).

1835, *Handb. Ent.* 2 : 106.

Type—*Dorydium paradoxum* Burmeister (Cape of Good Hope).

Notocephalius Jacobi.

1909, *Faun. S.W. Aust., Michaelsen u. Hartmeyer* 2 : 339.

Type—*Notocephalius hartmeyeri* Jacobi (South-West Australia).

Paracephaleus Evans.

1942, *Proc. Roy. Soc. Queensland* 54 : 49.

Type—*Paracephaleus montanus* Evans (Tasmania).

Procephaleus Evans.1937—*Pap. Roy. Soc. Tasm.* 1936 : 43.Type—*Procephaleus bulbosa* Evans (Western Australia).*Taxonomic Notes.*

At one time confusion existed between the identity of *Cephalelus* and *Paradorydium*. This is because, not only do species in these two genera superficially resemble each other, but Burmeister originally gave the name *Dorydium* to two distinct genera. One of these genera is a synonym of *Cephalelus*, whilst for the other (1838) Kirkaldy in 1901 proposed the new name *Paradorydium*. The matter has been discussed by Kirby (1894). Oshanin (1912) placed *Cephalelus* in the JASSINAE, Acocephalaria; Kirkaldy (1907) and Myers (1923) placed both *Cephalelus* and *Paradorydium* in the Cephalelini and CEPHALELINAE respectively, while Naudé (1926) placed *Cephalelus*, together with *Dorydium*, in the Jassini, Dorydiaria. Haupt (1929) referred *Cephalelus* to the EUPELICINAE together with *Dorydium*, *Cephalius* and *Dorycephalus*, whilst I previously (1939*b*) have considered the CEPHALELINAE as a sub-family of the LEDRIDAE.

Discussion of the ULOPINAE.

The ULOPINAE, as I have already suggested, may lie at the base of one of the lines of jassid descent. Evidence in support of this hypothesis is furnished by their small size, the primitive features retained in the structure of their heads and male genitalia, and also because they present a unique assemblage of secondary features, some of which are found also in other groups which are not closely inter-related. Such features include the development of thimble-like pits, the presence of short white hairs, and the transverse ridge which separates the ocelli from the face of the head.

Their distribution and their habits also suggest that the present representatives are the lingering remnants of a once extensive and universally distributed group.

Of the three tribes, the Ulopinini are the least, and the Cephalelini the most, specialised. Such features as the ULOPINAE share with the AETALIONIDAE are those due to a lack of specialisation in both groups, and the reason for the association of the former sub-family with the JASSIDAE is because its representatives have the same basic venation of the tegmen as the jassids.

Species in the genus *Moonia* retain the greatest number of primitive characters, since, as well as having well-defined maxillary sutures, their ocelli are in marginal depressions and not on the crown as they are in most of the Ulopinini and in all the Cephalelini. The occurrence of the ocelli on the crown, while the frons remains entirely ventral, is an unusual development. Such forms as feed on moss, reeds and rushes usually lack powers of flight and may never have acquired those of jumping, this being doubtless a secondary specialisation associated with the acquisition of an arboreal habitat.

LEDRINAE.⁸

Four tribes, the Ledrini, Stenocotini, Koebeliini and Thymbrini, are associated together in this sub-family and all are, in my opinion, early derivatives from the Ulopine stem. These tribes comprise large somewhat flattened, arboreal leaf-hoppers which are mostly brown, black or green in colour, although a few of the Ledrini are pink, and others brown with a yellow pattern development.

Ledrini⁸ (fig. 4).*Distribution.*

The Ledrini occur principally in the Oriental, African and Australian regions, but they also have a few representatives in the Nearctic and Neotropical regions and one (*Tetigonia* (*Ledra*) *aurita* L.) in the Palearctic region.

Size, Coloration and General Appearance.

The smallest representative of the Ledrini is 5 mm. long and the largest (*Ledromorpha planirostris* Donovan) 30 mm. long. In colour they are various shades of brown, green, and pinkish, and they usually lack a pattern development. Some are pitted on the head and thorax, others rugose, and a few have a covering of sparse white hairs. Typical ledrids have spatulate heads, ocelli on the crown, tegmina with reticulate venation and hind tibiae which are considerably flattened.

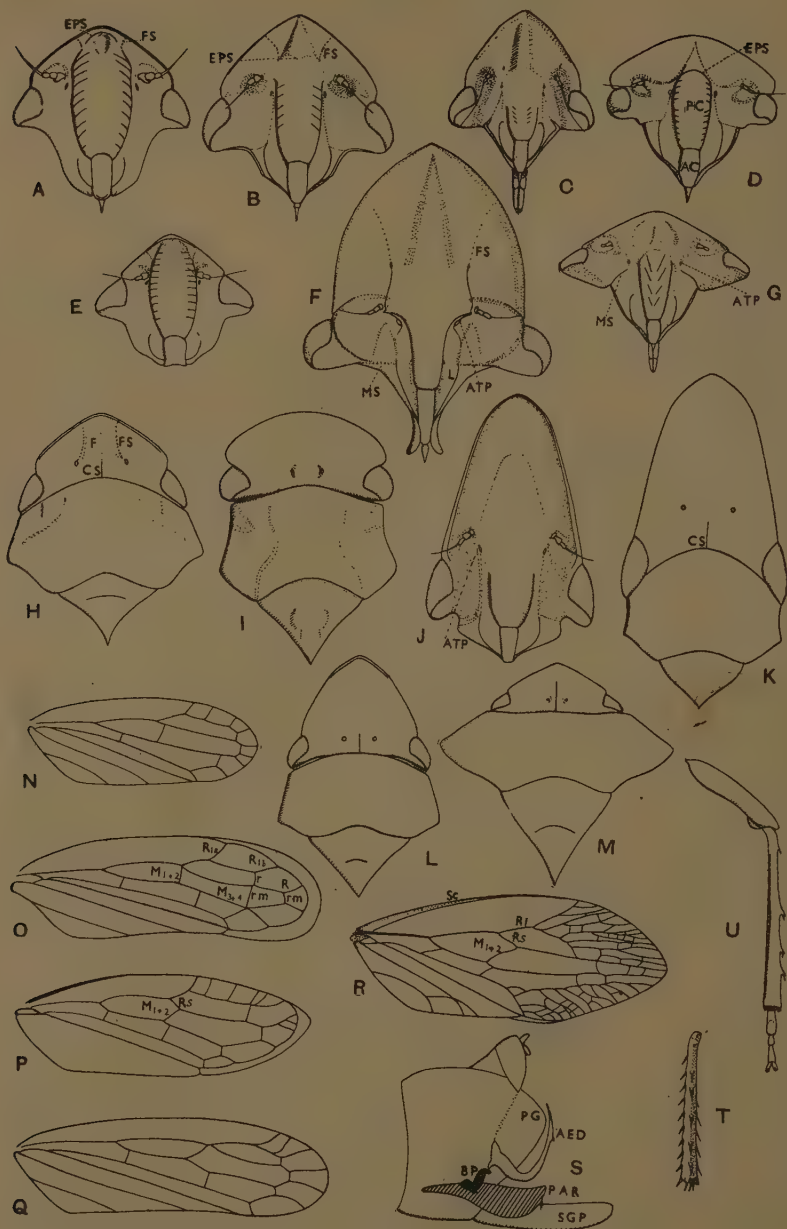
Food-plants and Habits.

Chatterjee (1934) has given a detailed account of the life-history and habits of *Petaloccephala nigrilinea* Walker in India and has listed the recorded food-plants; these show that this species is polyphagous, though exclusively arboreal. *Ledropsis rubromaculata* Laidlaw (1930) feeds and breeds on *Acacia catechu* in India and *Tetigonia aurita* occurs on oaks in Europe. All the Australian species, so far as is known, feed on eucalypts. *Xerophloea viridis* Fabricius, which occurs in North and South America and is especially abundant in arid regions, is a grass feeder (Osborn, 1935), but apparently also feeds on other low-growing plants (Knowlton and Allen, 1936). The nymphs of the Ledrini, which like the adults are considerably flattened, are capable of jumping if disturbed.

Description.

Head. The head may be long, spatulate and ventrally concave, or short, wide and medially convex. The labium is short, and the ante-clypeus is separated from the post-clypeus by a transverse suture. The lora may be linked by a ridge, sometimes identifiable as a suture, with the anterior tentorial pits (which are invariably exposed). The maxillary plates are usually narrow, but in *Xerophloea* and *Proranus* they are of moderate width, and the maxillary sutures may be distinct, vestigial, or absent. The post-clypeus is narrow,

⁸ China and Fennah (1946) have pointed out that *Ledra* F. is a synonym of *Tetigonia* Geoffroy, hence the group name would more correctly be the TETIGONINAE. As both these generic names have for so long been associated with well-known and well-defined groups, I am retaining the group name LEDRINAE in order to avoid needless confusion.



and, though the epistomal suture may be well defined, frontal sutures are seldom, and post-frontal sutures never, retained. The frons lies partly on the face and partly on the crown, and frontal sutures, if present, diverge posteriorly towards the sides of the head. The sides of a raised central posterior region of the face, which occurs in some species, mark the limits of the attachment of the dilator cibarial muscles. The antennae are short and the antennal ledges, if retained, are widely arched and ill-defined; usually they are entirely lost and the antennal depressions shallow. The ocelli, which are on the crown, are closer to the hind than to the anterior margin, and the coronal suture is usually, but not invariably, present. The eyes are prominent and sometimes globose.

Thorax. The pronotum, which is usually declivous anteriorly, is collar-like, and may have lateral, or dorsal, flap-like extensions.

Legs. The tibiae may be quadrilateral in section or flattened to a varying extent. The hind tibiae bear one or a few widely spaced spines mounted on prominent bases, and they may have additional rows of strong spines or a fringe of hair-like spines, and they are terminated by a double row of strong transverse spines.

Tegmina. The tegmina may have complete venation, a few additional cross-veins especially in the costal area, or have reticulate venation; and the appendix may be small, or wide and continue around the apex of the tegmen.

Male Genitalia. The male genitalia of only a limited number of species have been examined. All these had parallel-sided sub-genital plates, wide pygophores lacking processes, and the sternum of the ninth segment fused with the tergum.

Genera comprised in the Ledrini.

Bascarrhinus Fowler.

1898, *Biol. Centr. Amer. (Hem.)* 2 : 214.

Type—*Bascarrhinus platypoides* Fowler (Panama).

Camptelasmus Spinola.

1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 96, 150.

Type—*Camptelasmus caffer* Spinola (South Africa).

Chatura Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 176.

Type—*Chatura nigella* Distant (Ceylon).

Confucius Distant (synonym of *Ezrana* Distant).

1907, *Ann. Soc. ent. Belg.* 51 : 191.

Type—*Confucius granulatus* Distant (Hong Kong).

Dusuna Distant.

1907, *Ann. Soc. ent. Belg.* 51 : 188.

Type—*Dusuna morwhoti* Distant (Siam).

Eleazara Distant.

1907—*Faun. Brit. Ind. Rhyn.* 4 : 182.

Type—*Eleazara aedificatura* Distant (Assam).

Eogypona Kirkaldy (synonym of *Petaloccephala* Stål).

1901, *Entomologist* 34 : 38.

Type—*Eogypona kirbyi* Kirkaldy (Ceylon).

FIG. 4.

A, *Xerophloea viridis* F., head; B, *Camptelasmus hyalinus* Ev., head; C, *Petaloccephala perductalis* Dist., head; D, *Tetigonia cingalensis* Dist., head; E, *Proranus godmani* Fowler, head; F, *Ledromorpha planirostris* Don., head; G, *Tituria planata* F., head; H, *Xerophloea viridis*, head and thorax, dorsal aspect; I, *Tetigonia cingalensis*, head and thorax, dorsal aspect; J, *Rubria coccinea* Butler, head; K, *R. coccinea*, head and thorax, dorsal aspect; L, *Petaloccephala perductalis*, head and thorax, dorsal aspect; M, *Tituria planata*, head and thorax, dorsal aspect; N, *Camptelasmus hyalinus*, tegmen; O, *Xerophloea viridis*, tegmen; P, *Proranus godmani*, tegmen; Q, *Rubria coccinea*, tegmen; R, *Ledromorpha planirostris*, tegmen; S, *Ledracephala brevifrons* Walk., male genitalia; T, *Xerophloea viridis*, hind tibia; U, *Tituria planata*, hind leg.

- Epiclides* Amyot and Serville (preoccupied, see *Proranus* Spinola).
1843, *Hist. Nat. Ins. Hemipt.* : 577.
Type—*Ledra planata* Fabricius⁹ (India).
- Ezrana* Distant.
1907, *Faun. Brit. Ind. Rhyn.* 4 : 177.
Type—*Ezrana pygmaea* Distant (Bombay).
- Funkikonina* Kato.
1931, *Dobuts. Zasshi* 43, No. 512 : 438.
Type—*Ledra tuberculata* Kato (Formosa).
- Gudwana* Distant (synonym of *Porcorhinus* Goding).
1907, *Ann. Mag. nat. Hist.* (8) 20 : 189.
Type—*Gudwana typica* Distant (New South Wales.)
- Hemipeltis* Spinola.
1852, Gay, *Hist. Fis. y. Pol. de Chile, Zool.* 7 : 301.
Type—*Hemipeltis chilensis* Spinola (Chile).
- Jukaruka* Distant.
1907, *Ann. Soc. ent. Belg.* 51 : 190.
Type—*Jukaruka typica* Distant (Queensland).
- Ledra* Fabricius (synonym of *Tetigonia* Geoff., China and Fennah, 1946).
1803, *Syst. Rh yng.* pp. vii, 24.
Type—*Cicada aurita* Linnaeus (Europe) (Latreille, 1807).
- Ledracephala* Evans.
1947, *Trans. R. ent. Soc. Lond.* 98 : 252.
Type—*Ledra brevifrons* Walker (Australia).
- Ledromorpha* Stål.
1864, *Ann. Soc. ent. Fr.* (4) 4 : 68.
Type—*Fulgora planirostris* Donovan (Australia).
- Ledropsis* White.
1844, *Ann. Mag. nat. Hist.* 14 : 425.
Type—*Ledropsis cancruma* White (Hong Kong).
- Mesodiscus* Fieber (synonym of *Xerophloea* Germar).
1866, *Verh. zool.-bot. Ges. Wien.* 16 : 501.
Type—*Mesodiscus foveolatus* Fieber (America).
- Midoria* Kato.
1931, *Dobuts. Zasshi.* 43, No. 512 : 439.
Type—*Midoria capitata* Kato (Formosa).
- Neotituria* Kato.
1932, *Kontyu* 5 : 221.
Type—*Ledropsis kongosana* Matsumura.
- Pachyledra* Schumacher (synonym of *Petalocephala* Stål).
1912, *Wien. ent. Ztg.* 31 : 248.
Type—*Pachyledra kamerunensis* Schumacher (Cameroons).
- Parapetalocephala* Kato.
1931, *Dobuts. Zasshi* 43, No. 512 : 435.
Type—*Parapetalocephala montana* Kato (Formosa).
- Parapholis* Uhler (synonym of *Xerophloea* Germ.).
1877, *U.S. Geol. Survey* 3 : 461.
Type—*Parapholis peltata* Uhler (North America).
- Petalocephala* Stål.
1853, *Öfvers. Vetens-Akad. Förh. Stockh.* 1853 : 266, 1854 : 251.
Type—*Petalocephala bohemani* Stål (Java).

⁹ Both Stål (1866) and Distant (1907) have pointed out that the characters given by Amyot and Serville for their genus *Epiclides* are such, that *Ledra planata* Fabricius cannot be included in it.

Platyhynna Berg.1884, *Hemipt. Argent., Addenda*, p. 162.Type—*Epiclinae bdellostoma* Berg (Argentina).*Platyledra* Evans.1937, *Pap. Roy. Soc. Tasm.* 1936 : 39.Type—*Platyledra hirsuta* (South Australia).*Porcorhinus* Goding.1903, *Proc. Linn. Soc. N.S.W.* 27 : 38.Type—*Porcorhinus mastersi* Goding (New South Wales).*Proranus* Spinola.1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 1852 : 97, 162.Type—*Proranus ghilianii* Spinola (Para).*Rubria* Stål.1865, *Öfvers. Vetens-Akad. Förh. Stockh.* 1865 : 158.Type—*Petaloccephala sanguinosa* Stål (North Australia).*Tetigonia* Geoffroy.1762, *Hist. abr. Ins.* p. 429.Type—*Cicada aurita* Linnaeus (Europe).*Tettigoniella* Jacobi (synonym of *Tetigonia* Geoff.).1903, *Zool. Jahrb.* 19 : 778.*Thalasia* Germar.1836, *Silb. Rev. Ent.* 4 : 71.Type—*Thalasia brunnepennis* Germar (Cape of Good Hope).*Titia* Stål (see *Titiella* Bergroth).1866, *Hemipt. Africana* 4 : 105.Type—*Acocephalus punctiger* Stål (South Africa).*Titiella* Bergroth (new name for *Titia* Stål).1920, *Ark. Zool.* 12 (17) : 29.*Tituria* Stål.1865, *Öfvers. Vetens-Akad. Förh. Stockh.* 1865 : 158.Type—*Membracis planata* Fabricius (India).*Turititia* Schumacher.1912, *Wien. ent. Ztg.* 31 : 248.Type—*Turititia uniformis* Schumacher (Cameroons).*Xerophloea* Germar.1839, *Zeitsch. für Ent.* 1 : 190.Type—*Cercopis viridis* Fabricius (America).*Taxonomic Notes.*

Although as early as 1870 Stål had made use of the group name *Ledrina*, later authors continued to follow Dohrn (1859) and to refer *Ledra* to the family SCARIDAE (Fieber, 1875 ; Melichar, 1896 ; Ribaut, 1936), even although *Scaris* is related to *Gypona*, and not to *Ledra*.

Oman (1943) has created a sub-family of the JASSIDAE, the XEROPHLOENINAE, to contain *Xerophloea* : this genus had previously been placed in the GYPONINAE (Lawson, 1920 ; De Long and Caldwell, 1937) until 1941, when I referred it to the LEDRIDAE. *Rubria* is yet another ledrid genus which has been associated with *Gypona*, since Naudé, even although he recognised a sub-family, the LEDRINAE, referred *Rubria* to the GYPONINAE. Haupt (1929) was of opinion that *Thaumatoscopus*, which is related to *Penthimia*, should be included in the LEDRIDAE.

These various instances of the incorrect association of unrelated genera are examples of the outcome which attends classification based on a single character, the character in these cases being the position of the ocelli. If a comparison is made between Fig. 4 and Fig. 30 the significant differences between the Ledrini and the Gyponini will become immediately apparent.

Stenocotini (fig. 5).

Distribution.

Australia.

Size, Coloration and General Appearance.

The Stenocotini range in length from 6 to 18 mm. In colour they are brown, and their tegmina may display a pattern development or be transparent. Considerable sexual dimorphism occurs, and the males, which are smaller than the females, differ from them also in colour markings and in minor structural details.

Food-plants and Habits.

All feed exclusively on the trunks of eucalypts, and the nymphs, which are semi-transparent, flattened, and almost as thin as paper, are usually found concealed under bark.

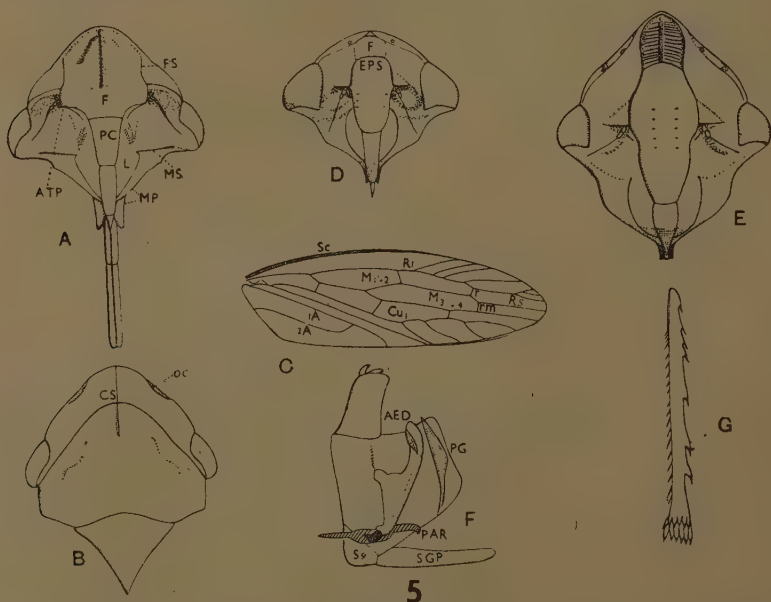


FIG. 5.

A, *Stenocotis depressa* Walk., head; B, *S. depressa*, head and thorax, dorsal aspect; C, *S. depressa*, tegmen; D, *Kyphocotis brunneus* Ev., head; E, *Smicrocotis obscura* Kirk., head; F, *S. obscura*, male genitalia; G, *S. depressa*, hind tibia.

Description.

Head. The head is flat and wide and the labium long. The ante-clypeus, which is usually long and narrow and is sometimes recurved apically, is separated from the post-clypeus by a distinct or a vestigial transverse suture. The maxillary plates are of moderate width and their narrow anterior apices partially enfold the ante-clypeus; the maxillary sutures may be present or absent. The post-clypeus, which may be narrower than the frons, or of even width, is usually separated from the frons by a distinct, or a vestigial, epistomal suture, and the frons is always entirely facial in position. The antennae are short, the strong antennal ledges transverse, or widely arched, and the antennal depressions shallow. The ocelli are either sunk in ventral, marginal, or dorsal depressions, or lie posterior to a transverse ridge, which joins the eyes close to the hind margin of the face. The eyes are prominent and sometimes globose.

Thorax. The pronotum, which may be declivous anteriorly, is approximately heart-shaped and narrow laterally.

Legs. The tibiae are quadrilateral in section and somewhat flattened. The hind tibiae, which are long, bear, in addition to three rows of short spines, a row of widely spaced spines mounted on prominent bases, which decrease in size from the apex of the tibia to the base. In addition, the hind tibia has two apical rows of strong transverse spines.

Tegmina. The venation of the tegmen does not conform to the usual jassid pattern, but differs in the development of a Y-vein in the clavus, the presence of additional costal veinlets, and in frequently having a first cubitus with more than the usual two branches.

Male Genitalia. The parameres are short, the sub-genital plates parallel-sided, and the pygophores, which are wide, bear a dorsally directed process. The separate identity of the ninth sternite is retained.

*Genera comprised in the Stenocotini.**Anacotis* Evans.

1937, *Mem. Queensland Mus.* 11 : 161.

Type—*Anacotis hackeri* Evans (Queensland).

Kyphocotis Kirkaldy.

1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 370.

Type—*Kyphocotis tessellata* Kirkaldy (Queensland).

Ledracotis Evans.

1937, *Mem. Queensland Mus.* 11 : 162.

Type—*Ledracotis gunnensis* Evans (New South Wales).

Smicrocotis Kirkaldy.

1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 370.

Type—*Smicrocotis obscura* Kirkaldy (Queensland).

Stenocotis Stål.

1854, *Öfvers. Vetens-Akad. Förh. Stockh.* 1854 : 254.

Type—*Stenocotis subvittata* Stål (= *Ledra depressa* Walker, Stål, 1862, Kirkaldy, 1906) (Australia).

Taxonomic Notes.

The relationship which exists between the Ledrini and the Stenocotini has been accepted previously (Kirkaldy, 1906; Distant, 1907). Baker (1923), who noted the affinity between *Stenocotis*, *Ulopa*, *Paropia* and *Koebelia*, was of the opinion that *Signoretia*, *Euacanthus* and *Pythamus* belonged to the same complex. Haupt (1929) referred *Stenocotis* to the PAROPIINAE, a sub-family which he placed in the JASSIDAE and not in the LEDRIDAE.

Koebeliini (fig. 6).*Distribution.*

Western North America.

Size, Coloration and General Appearance.

Koebelia californica Baker is 5 mm. long and dark brown in colour, with an obscure pattern of pale brown and white markings; in shape, it is moderately flattened.

Food-plants and Habits.

K. californica occurs on pines.

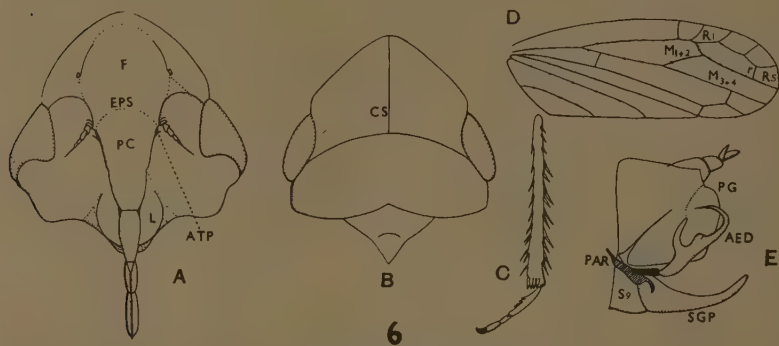


FIG. 6.—*Koebelia californica* Baker.

A, head; B, head and thorax, dorsal aspect; C, hind tibia and tarsus; D, tegmen; E, male genitalia.

Description.

Head. The head is flattened, the labium is of moderate length and the maxillary plates are wide. The frons is wider than the post-clypeus and lies entirely on the face of the head. The antennae are short, the antennal ledges weak and widely arched, and the antennal depressions shallow. The ocelli lie alongside the frons.

Thorax. The pronotum, which is short, is wide laterally.

Legs. The tibiae are quadrilateral in section. The hind tibiae have two rows of evenly spaced spines set on prominent bases and two rows of small unmounted spines.

Tegmina. The venation is of the usual jassid type, but for the presence of additional costal veinlets, and raised dots occur alongside the veins.

Male Genitalia. The parameres are short and the ninth sternite retains its separated identity.

Genera comprised in the Koebeliini.

Koebelia Baker.

1897 *Psyche* 8 : 76.

Type—*Koebelia californica* Baker (California).

Taxonomic Notes.

The isolated position of this genus with respect to the rest of the JASSIDAE has always been appreciated, likewise its position close to such

genera as *Stenocotis*. Oshanin (1912) recognised a group, the Koebeliaria, of which he considered *Adelungia* to be a component. Baker (1923), who considered that *Koebelia* lay between *Stenocotis* and *Ulopa*, created a family, the KOEBELIIDAE, for its reception. Both Haupt (1929) and De Long and Caldwell (1937) included *Koebelia* in the PAROPIINAE, a sub-family of the JASSIDAE.

Thymbrini (fig. 7).

Distribution.

Australia, New Guinea and New Zealand.

Size, Coloration and General Appearance.

The Thymbrini range in length from 5 to 16 mm. and in colour they are various shades of black, brown, orange and green, and they often have a mottled appearance. They are strongly built, somewhat flattened insects, and the nymphs also are usually flattened.

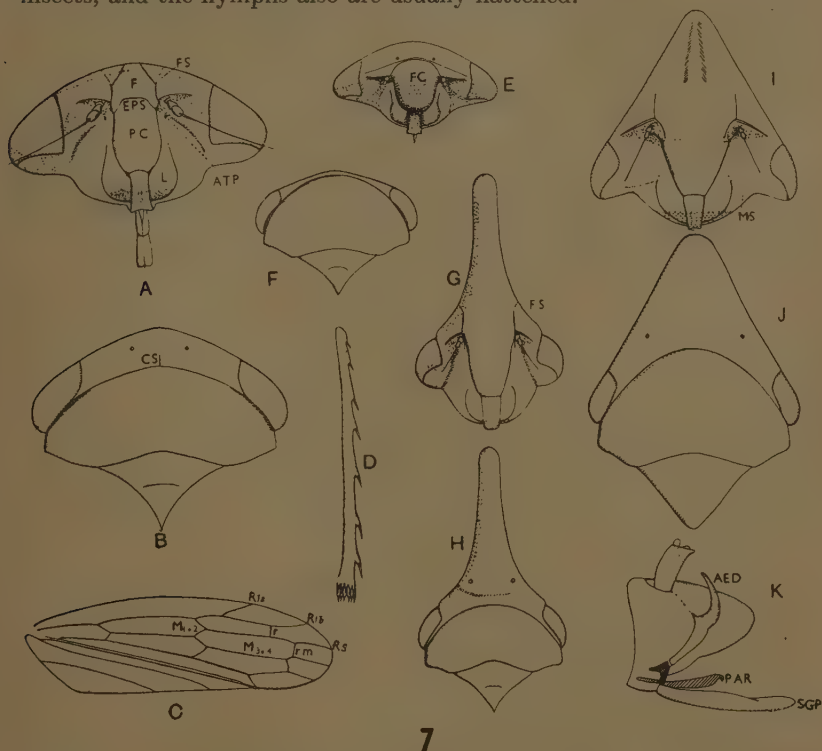


FIG. 7.

A, *Novothymbris zealandica* Myers, head; B, *N. zealandica*, head and thorax, dorsal aspect; C, *Rhotidus cuneatus* Walk., tegmen; D, *R. cuneatus*, hind tibia; E, *Macroceps fasciatus* Sign., head; F, *M. fasciatus*, head and thorax, dorsal aspect; G, *Ledraprora compressa* Ev., head; H, *L. compressa*, head and thorax, dorsal aspect; I, *Rhotidus cuneatus*, head; J, *R. cuneatus*, head and thorax, dorsal aspect; K, *Macroceps tonnoiri* Ev., male genitalia.

Food-plants and Habits.

Although Kirkaldy has recorded *Epipsychidion epipyropis* Kirkaldy from *Leptospermum*, it is certain that the greater number of the Australian representatives feed on eucalypts. The New Zealand species are likewise arboreal.

Description.

Head. The head varies considerably in shape. The labium is of moderate length, and the ante-clypeus, which is long and narrow, is recurved anteriorly or depressed below the level of the lora and the post-clypeus. The maxillary plates are of moderate width and vestigial maxillary sutures may be discernible. The frons, which may be a distinct sclerite or have lost its separate identity, may be entirely facial in position, or extend on to the crown. The antennae are usually short but may extend beyond the sides of the head, and the antennal ledges, which are strong, are either transverse or oblique; the antennal depressions are of moderate depth. The ocelli are situated on the crown, and in those species in which the head is not produced they are separated from the hind margin of the frons or fronto-clypeus by a well-defined transverse ridge which extends laterally as far as the eyes, and which may be marginal in position. (In the illustration of *Macroceps fasciatus* Signoret, fig. 7e, the ocelli appear to lie on the face, but that part of the head which occurs above the antennal ledges is actually part of the crown, and forms an even curved surface with the declivous pronotum.)

Legs. The tibiae are quadrilateral in section and the hind tibiae, which are often long and slender, bear a row of strong spines mounted on prominent bases which decrease in size from the apex of the tibia to the base. They have also, as well as rows of smaller spines, a double row of apical transverse spines.

Tegmina. The venation of the tegmen is complete and the appendix is small.

*Genera comprised in the Thymbrini.**Alseis* Kirkaldy.

1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 30, 37.

Type—*Alseis osborni* Kirkaldy (Queensland).

Epipsychidion Kirkaldy.

1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 345.

Type—*Epipsychidion epipyropis* Kirkaldy (New South Wales).

Hackeriana Evans.

1937, *Pap. Roy. Soc. Tasm.* 1936 : 67.

Type—*Hackeriana huonensis* Evans (Tasmania).

Ledraprora Evans.

1937, *Pap. Roy. Soc. Tasm.* 1936 : 40.

Type—*Ledraprora insularis* Evans (Kangaroo Island, South Australia).

Ledrella Evans.

1937, *Pap. Roy. Soc. Tasm.* 1936 : 40.

Type—*Ledrella brunnea* Evans (Victoria).

Macroceps Signoret.

1879, *Ann. Soc. ent. Fr.* 9 : 53, 10 : 363.

Type—*Macroceps fasciatus* Signoret (Australia).

Macrometopius Horvath (invalid emendation of *Macroceps* Sign.).

1914, *Ann. Mus. Nat. Hung.* 12 : 660.

Mitelloides Evans.

1939, *Trans. Roy. Soc. S. Aust.* 63 : 46.

Type—*Mitelloides moaensis* Evans (Banks Island, Torres Strait).

Novothybris Evans.1941, *Trans. Roy. Soc. N.Z.* 71 : 162.Type—*Diedrocephala zealandica* Myers (New Zealand).*Putoniessa* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 50.Type—*Putoniessa dignissima* Kirkaldy (New South Wales).*Rhotidus* Stål (synonym of *Rhotidus* Walker).1865, *Öfvers. Vetens-Akad. Förh. Stockh.* 22 : 157.Type—*Rhotidus navicula* Stål (Queensland).*Rhotidoides* Evans.1937, *Pap. Roy. Soc. Tasm.* 1936 : 59.Type—*Rhotidoides norfolkensis* Evans (Tasmania).*Rhotidus* Walker.1862, *J. Ent.* 1 : 318.Type—*Rhotidus cuneatus* Walker (Queensland).*Thymbris* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 49.Type—*Thymbris inachis* Kirkaldy (Queensland).*Taxonomic Notes.*

Ignorance of the genotype has led to confusion in the past respecting the position of *Rhotidus*, and both Kirkaldy (1906) and Distant (1907) referred this genus to the LEDRINAE. The seven new species of *Rhotidus* described by Kirkaldy almost certainly belong to the genus *Rubria* and not to *Ledropsis*, with which genus Kirkaldy (1907) believed *Rhotidus* might be synonymous. *Epipsychidion* was originally placed in the AGALLIINAE (=BYTHOSCOPIINAE auctt.) and *Alseis*, *Thymbris* and *Putoniessa* in the Eurymelini (which also, in the sense used by Kirkaldy, =BYTHOSCOPIINAE auctt.). The last named genus, Kirkaldy suggested, formed a complete link between the JASSIDAE and the BYTHOSCOPIDAE and pointed the way to the STENOCOTINAE. Oshanin (1912) referred *Macroceps* to the JASSINAE, Acocephalaria, and Baker (1919) associated *Thymbris* and *Tartessus* in a tribe, the Tartessusaria; Haupt (1929) placed *Thymbris* in the EUSCELIDAE. Of the genera described by me, *Ledrella* and *Ledraprora* were originally placed in the LEDRINAE and the rest in the EUSCELIDAE, and it was not until 1939b that I recognised the distinctive features of the group and created a new family, the THYMBRIDAE.

Discussion of the LEDRINAE.

I have already mentioned, that because of the lack of a common characteristic peculiar to the group, I have found it impossible to devise an adequate definition of this sub-family. In consequence I have been forced to make use of groups of overlapping characters in order to establish inter-relationships.

Two of the principal, though not universal, characteristics of the Ledrini are spatulate heads with dorsal ocelli, and flattened hind tibiae with a sparse armature of spines. The four major distinguishing characters of the Stenocotini are ocelli in marginal depressions; a Y-vein in the clavus; a first cubitus with more than two branches,

and hind tibiae which have one row of spines mounted on widely spaced, prominent bases. *Ledromorpha planirostris* has a spatulate head, dorsal ocelli and flattened tibiae, and a tegmen which, in common with several other representatives of the Ledrini, has reticulate venation. It would thus appear as if the association of this species with *Ledra* and related genera was amply justified. If, however, the figure of the head of *L. planirostris* (fig. 4f) is compared with that of *Stenocotis depressa* (fig. 5a) the resemblance between the two heads will be seen to be so striking as to suggest that close genetic affinity exists between these species. The resemblance is supported by characters supplied by the tegmina, since the tegmen of *L. planirostris*, like that of nearly all the Stenocotini, has a first cubitus with several branches. Hence it is apparent that *Ledromorpha* could be referred, with equal justification, either to the Ledrini or to the Stenocotini.

That *Koebelia californica* is related to *Stenocotis depressa* is evident from the close similarity existing between the heads of these two insects. With each, the head is wide and flattened, the antennal depressions shallow, the antennal ledges widely arched, and the frons extensive and entirely ventral in position.

The Thymbrini cannot so readily be associated with the other tribes comprised in the LEDRINAE, nevertheless they undoubtedly belong to the same complex. They resemble the Ledrini in having acquired green as a secondary colour, and also in having lora that have retained their original association with the tentorial pits. They resemble both the Ledrini and the Stenocotini in having flattened nymphs, some of which may have foliaceous heads, and in the position of their ocelli on the crown of the head. They resemble the Stenocotini in the shape and armature of their hind tibiae, in the possession of an ante-clypeus which is recurved apically and in having a transverse ridge, either on the face or on the margin of the head; this ridge, which lies anterior to the ocelli, denotes descent from forms which had ocelli sunk in marginal depressions. Unlike the other tribes of the LEDRINAE, the Thymbrini have tegmina with complete, normal, venation.

Although representatives of the Thymbrini now occur in all parts of Australia, as well as in New Zealand, it is probable that their original development took place in the eastern, and not in the western, part of the continent.

HECALINAE.

Four tribes are associated in this sub-family, the Hecalini, Dorycephalini, Eupeliciini and Paradorydiini. The majority of the representatives are brown in colour, but some are green, and a few green with orange markings. The head is usually widely, or narrowly, produced and emarginate beneath the eyes. The labium is short, the antennal ledges vestigial, or absent, and the ocelli either marginal or on the crown, close to the anterior margin of the head. The post-clypeus either occupies all the frontal region of the face, or in instances where the frontal sutures diverge widely in a lateral direction it extends only on to the central

area. The greater part of the crown is of frontal origin, but postfrontal sutures are absent. The pronotum is usually collar-like and sometimes carinate.

Hecalini (fig. 8).

Distribution.

All the principal geographical regions.

Size, Coloration and General Appearance.

The Hecalini range in length from 4.5 to 11 mm. and in colour are either some shade of brown, varying from pale straw to almost black, or they are pale yellow or green, with or without orange markings. The crown and pronotum are flat, and the head is often shovel-shaped and ventrally convex. In some species strong sexual dimorphism occurs.

Food-plants and Habits.

So far as is known, the Hecalini are all grass-feeders, and some species are restricted in their choice of grasses: thus Osborn and Ball (1897) record *Hecalus lineatus* Uhler from *Spartina* and *Parablocratus viridis* Uhler from *Stipa*.

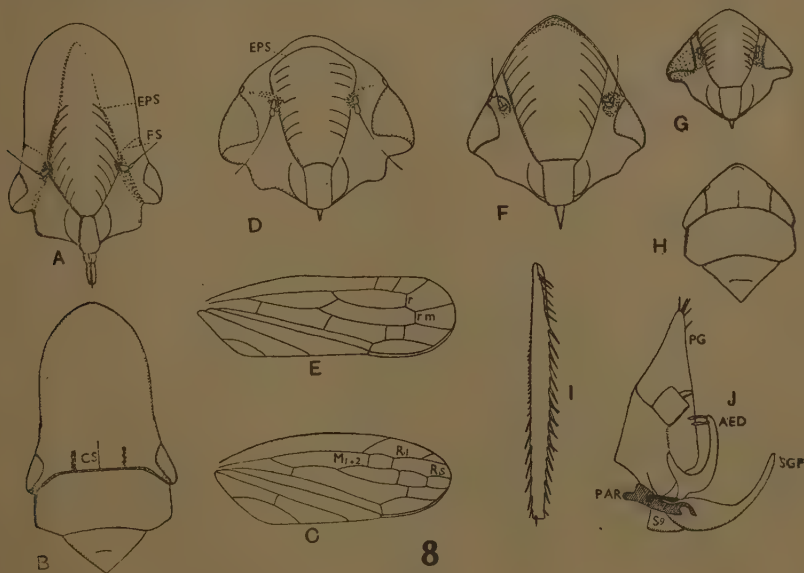


Fig. 8.

A, *Hecalus kuthyi* Toth., head; B, *H. kuthyi*, head and thorax, dorsal aspect; C, *H. kuthyi*, tegmen; D, *Bordesia mitrata* Bergev. (♂), head; E, *B. mitrata*, tegmen; F, *Parablocratus viridis* Uhl., head; G, *Parablocratus citrinus* Ev., head; H, *P. citrinus*, head and thorax, dorsal aspect; I, *Hecalus lineatus* Uhl., hind tibia; J, *H. lineatus*, male genitalia.

Description.

Head. In sexually dimorphic species the males have short, and the females long, heads. The labium is short and the maxillary plates wide: the epistomal suture, when discernible, is either narrowly, or widely, arched and it may coincide posteriorly with the hind margin of the face. The frontal sutures, if retained, are directed towards the ocelli, and in such heads as are not produced, these sutures lie alongside part of the arched epistomal suture. In forms with produced and apically spatulate heads, the frontal sutures diverge laterally, hence they do not coincide with any part of the epistomal suture: postfrontal sutures, which, if present, would occur on the crown, are not retained. The antennal ledges are vestigial or absent, the antennal depressions shallow, and the ocelli, which are situated on the narrow anterior margin of the head, are usually either in contact with the eyes or else very close to them.

Thorax. The pronotum is collar-like and dorsally flattened.

Legs. The fore and middle tibiae are rounded, and the hind tibiae are flattened and have three rows of strong, even spines in addition to a row of slender spines.

Tegmina. The tegmina are rounded apically and the venation is usually of the normal jassid type, except that additional cross-veins may be present, especially in the costal region. The tegmina of male insects are sometimes shorter than those of female insects, even though true brachyptery seldom occurs.

*Genera comprised in the Hecalini.**Annidion* Kirkaldy.

1905, *Wien. ent. Ztg.* **24** : 267.

Type—*Annidion pulcherrimum* Kirkaldy (Ivory Coast).

Bergiella Baker (synonym of *Spanbergiella* Sign.).

1897, *Canad. Ent.* **29** : 157.

Type—*Parabolocratus uruguayensis* Berg (Uruguay).

Bonamus Oman.

1936, *Univ. Kansas Sci. Bull.* **24** : 365.

Type—*Bonamus lineatus* Oman (Argentina).

Bordesia Bergevin.

1929, *Bull. Soc. Hist. nat. Afr. Nord.* **20** : 7.

Type—*Bordesia mitrata* Bergevin (North Africa).

Cerillus Oman.

1936, *Univ. Kansas Sci. Bull.* **24** : 362.

Type—*Hecalus notatus* Osborn (Brazil).

Chelusa Signoret.

1879, *Ann. Soc. ent. Fr.* **9** : 51, **10** : 51.

Type—*Acocephalus madagascarensis* Signoret (Madagascar).

Clavena Melichar.

1902, *Ann. Mus. zool. St. Petersb.* **1902** : 127.

Type—*Clavena sulcata* Melichar (West China).

Columbanus Distant (synonym of *Ledrotypa* Distant).

1916, *Faun. Brit. Ind. Rhyn.* **6** : 224.

Type—*Columbanus misranus* (Bengal).

Dicyphonia Ball.

1899, *Proc. Iowa Acad. Sci.* **7** : 69.

Type—*Dicyphonia pamentosa* Ball (emended to *ramentosa*, Van Duzee, 1917) (North America).

Ectomops Signoret.

1879, *Ann. Soc. ent. Fr.* **9** : 51, **10** : 49.

Type—*Ectomops chinensis* Signoret (China).

Egenus Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 363.Type—*Egenus acuminatus* Oman (Argentina).*Eremitopius* Lindberg.1927, *Notulae Ent.* 7 : 29.Type—*Eremitopius albus* Lindberg (Turkestan).*Glossocratus* Fieber (synonym of *Hecalus* Stål).1866, *Verh. zool.-bot. Ges. Wien.* 16 : 502.Type—*Glossocratus foveolatus* Fieber, 1872 (South Russia).*Hecalus* Stål.1864, *Ann. Soc. ent. Fr.* (4) 4 : 65.Type—*Petaloccephala paykulli* Stål (Senegal).*Ledrotypa* Distant.1912, *Ann. Mag. nat. Hist.* (8) 10 : 442.Type—*Ledrotypa spatulata* Distant (Himalayas).*Neoslossonia* Van Duzee.1909, *Bull. Buff. Soc. nat. Sci.* 9 : 218.Type—*Neoslossonia atra* Van Duzee (= *putnami* Osborn) (North America).*Parabolocratus* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 502.Type—*Parabolocratus glaucescens* Fieber (Palearctic Region).*Parabolitus* Naudé.1926, *S. Africa Dept. Agric. Ent. Mem.* 4 : 37.Type—*Parabolitus anceps* Naudé (South Africa).*Psegmatus* Fieber (Signoret).1872, Fieber, *Cat. Eur. Cicad.* p. 10 : *Rev. Mag. Zool.* 1875 : 402.1880, Signoret, *Ann. Soc. ent. Fr.* (5) 10 : 46.Type—*Psegmatus lethierryi* Fieber (Signoret) (South Russia).*Spanbergia* Signoret (see *Spanbergiella* Sign.).1879, *Ann. Soc. ent. Fr.* (5) 9 : 51.Type—*Glossocratus vulneratus* Uhler (North America).*Spanbergiella* Signoret (valid emendation of *Spanbergia* Signoret).1879, *Ann. Soc. ent. Fr.* (5) 9 : 273.*Tenucephalus* De Long1944, *Ohio J. Sci.* 44 : 236.Type—*Tenucephalus marginellus* De Long (Mexico).*Taxonomic Notes.*

Distant (1908), followed by Merino (1936) recognised a division, the Hecalusaria, to comprise not only *Hecalus* and related genera, but also *Nirvana*. Melichar (1903) and Lawson (1920) referred *Hecalus* to the Acocephalini, while Naudé (1926) referred it to the JASSINAE. Haupt (1929) gave the HECALINAE sub-family status, while Evans (1939a) and Oman (1943) considered the Hecalini as a tribe of the EUSCELINAE. Later (1939b) I referred *Hecalus* to the BYTHOSCOPIIDAE, being misled by its superficial resemblance to *Reuteriella*, a genus which has undoubted affinities with *Jassus* (*Bythoscopus*).

Dorycephalini (fig. 9).*Distribution.*

Russia and North America. (Kirkaldy, 1906, has described three

species of *Dorycephalus* from Australia, but these belong to the genus *Anacephaleus*.)

Size, Coloration and General Appearance.

The male of *Dorycephalus platyrhynchus* Osborn is 7 mm., and the female 10 mm. long, and while the former has fully developed tegmina the latter is brachypterous. Both sexes are pale brown in colour and have short white hairs on the head and pronotum.

Food-plants and Habits.

Ball (1920) has given an account of the life-history of *D. platyrhynchus* which breeds on wild rye (*Elymus*), feeds on grasses generally (Osborn, 1897), and overwinters in the nymphal stage. This is an unusual habit for leaf-hoppers, since they usually pass the winter either in the egg-stage or as hibernating adults.

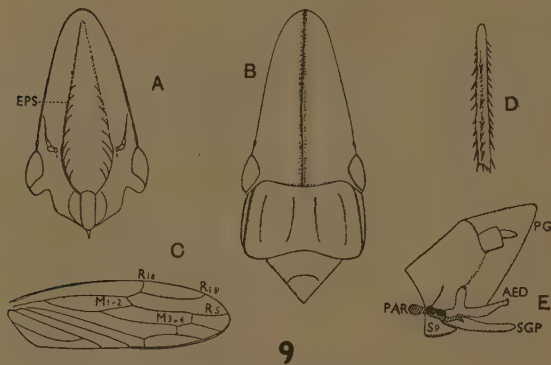


FIG. 9.—*Dorycephalus platyrhynchus* Osb.

A, head ; B, head and thorax, dorsal aspect ; C, tegmen ; D, hind tibia ; E, male genitalia.

Description.

Head. The head is shovel-shaped and emarginate beneath the eyes and the labium is short. The tentorial pits are exposed, the antennal ledges are not developed and the antennal depressions are shallow. The post-clypeus is produced posteriorly into the frontal region and no traces of frontal or postfrontal sutures remain. The ocelli lie close to the eyes, on the margin which separates the face from the crown.

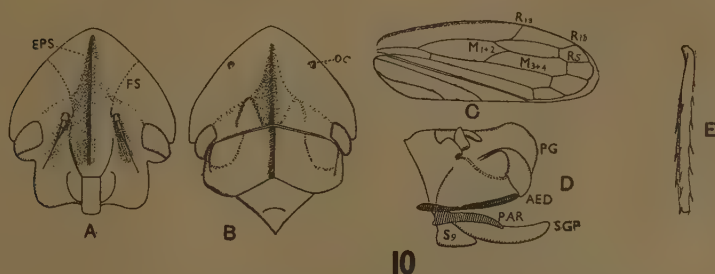
Thorax. The prothorax is collar-like and laterally carinate.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are flattened, have three rows of short, strong spines.

Tegmina. The tegmen has complete venation. (In fig. 9c cross-vein *r* is absent, but this feature is probably only an individual variation.)

*Genera comprised in the Dorycephalini.**Dorycephalus* Kouschakewitch.1866, *Hor. Soc. ent. Ross.* 4 : 102.Type—*Dorycephalus baeri* Kouschakewitch (S. Russia).*Semenovium* Kuznetsov.1928, *Zool. Anzeig.* 79 : 312.Type—*Semenovium ferganae* Kuznetsov (Turkestan).*Taxonomic Notes.*

Dorycephalus was placed in the Acocephalaria by Oshanin (1912), in the Acocephalini by Lawson (1920), in the EUPELICINAE by Haupt (1929), and together with *Hecalus*, in the DORYDIINAE by Medler (1942). In 1938b I referred it to the LEDRINAE, and Oman has placed it in a tribe of the EUSCELINAE, the Dorycephalini.

FIG. 10.—*Eupelix cuspidata* Fabr.

A, head ; B, head and thorax, dorsal aspect ; C, tegmen ; D, male genitalia ; E, hind tibia.

Eupelicini (fig. 10).*Distribution.*

Europe, North Africa and the Canary Islands.

Size, Coloration and General Appearance.

The Eupelicini range in length from 5 to 7 mm. and in colour are pale brown. Their wide foliaceous heads and the character of the extension of the vertex around the eyes are unique features, which enable their instant recognition.

Food-plants and Habits.

Melichar (1896) records *Eupelix cuspidata* Fabricius and *E. producta* Germar as occurring in dry clearings and on stretches of moorland ; Haupt (1935) as occurring in dry grassy places ; while Edwards (1896) states that the former is found at the roots of low plants.

Description.

Head. The head is emarginate beneath the eyes, the labium is short and the maxillary plates are wide and angulate. The antennae are short, the antennal ledges vestigial, or absent, and the antennal depressions are of moderate depth and limited extent. The post-clypeus, which is carinate, encroaches narrowly on to the frontal region and the vestigial frontal sutures diverge laterally towards the ocelli. The ocelli, which are on the crown close to the anterior margin, are sometimes raised on prominences: the coronal suture is distinct, but postfrontal sutures are absent.

Thorax. The pronotum is wide laterally and carinate.

Legs. The tibiae are quadrilateral in section and the hind tibiae are short, and have a sparse armature of weak spines.

Tegmina. The venation of the tegmen is complete and the veins are raised in relief.

Genera comprised in the Eupelicini.

Chloropelix Lindberg.

1936, *Comment. Biol.* 6 : 3.

Type—*Chloropelix canariensis* Lindberg (Canary Islands).

Eupelix Germar.

1821, *Mag. Ent.* 4 : 93.

Type—*Cicada cuspidata* Fabricius (Europe).

Taxonomic Notes.

Melichar (1896), Edwards (1896) and Oshanin (1912) referred *Eupelix* to the Acocephali, ACOCEPHALIDAE and Acocephalaria respectively: Haupt (1929) recognised the EUPELICINAE as a sub-family and later (1935) as a tribe of the JASSIDAE. In 1939*b* I grouped the EUPELICINAE as one of the sub-families of the LEDRIDAE.

Paradorydiini (fig. 11).

Distribution.

Widely distributed in the warmer regions of the Eastern Hemisphere.

Size, Coloration and General Appearance.

The Paradorydiini range in length from 2.5 to 10 mm., and in colour they are pale brown or green. In shape, most representatives are long and narrow, and have a head which is either arrow-shaped, or narrowly produced and apically spatulate: both the head and thorax are pitted. In appearance they resemble insects comprised in the Cepheleini, but this resemblance is essentially superficial. (Evans, 1937*a*, pl. 16.)

Food-plants and Habits.

Paradorydium westwoodi B. W. has been taken on rushes growing in damp situations in New Zealand (Kirby, 1894). In Australia *Delto-dorydium viridis* Evans has been collected from *Melaleuca* (a shrub); *D. cooki* Evans on *Echium plantagineum*; *Paradorydium menalaus* Kirkaldy on grass and *P. casuarinae* on *Casuarina*. In South Africa several species are apparently associated with grasses.

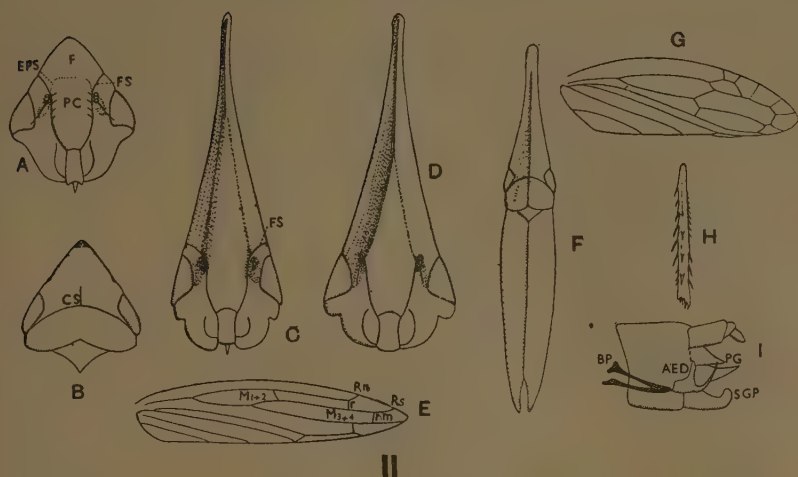


FIG. 11.

A, *Deltodorydium viridis* Ev., head; B, *D. viridis*, head and thorax, dorsal aspect; C, *Paradorydium angolensis* Ev., head; D, *Paradorydium lanceolatum* Burm., head; E, *P. lanceolatum*, tegmen; F, *P. lanceolatum*; G, *Deltodorydium viridis*, tegmen; H, *Paradorydium menalus* Kirk., male genitalia; I, *Paradorydium lanceolatum*, male genitalia.

Description.

Head. The labium is short and the maxillary plates are wide. A vestigial epistomal suture may be visible in short-headed forms, but is invariably absent in long-headed species, in which the post-clypeus is probably confined to the narrowly swollen hind portion of the face. The postfrontal sutures are curved towards the sides of the head, which they reach slightly posterior to the eyes. The antennae are short, the antennal depressions shallow, and antennal ledges are not developed. The ocelli, when present, are marginal in position, and while the coronal suture may be present, postfrontal sutures are never retained.

Thorax. The pronotum, which is of moderate width laterally, is rounded anteriorly, and medially emarginate posteriorly.

Legs. The tibiae are quadrilateral in section and the hind tibiae bear a few spines.

Tegmina. The tegmina are usually narrow apically and the veins are raised in relief. The venation is sometimes complete or there may be either more, or less, than the usual number of cross-veins.

Wings. Wings are present in the short-headed forms, but they are reduced, vestigial, or absent in those which have long heads.

Genera comprised in the *Paradorydiini*.

Bumizana Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 32.

Type—*Bumizana elongata* Distant (South India).

Carphosoma Royer (new name for *Dorydium* Burmeister, 1838, a synonym of *Paradorydium* Kirkaldy).

1907, *Bull. Soc. ent. Fr.* 1907 : 29.

Cephalius Fieber (Signoret).

1872, Fieber, *Cat. Eur. Cicad.* 10 : Fieber, *Rev. Mag. Zool.* 1876 : 402.

1879, Signoret, *Ann. Soc. ent. Fr.* (5) 9 : 60.

Type—*Cephalius frontalis* Fieber (Signoret) (North Africa).

Deltodorydium Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 73 (Evans, 1937a : 45).Type—*Paradorydium brighami* Kirkaldy (New South Wales).*Dorydium* Burmeister (see *Paradorydium* Kirk.).1838, *Gen. Ins. Rhyng.* 5 : 1838 ; 1839.Type—*Dorydium lanceolatum* Burmeister (Sicily).*Epicephalius* Matsumura.1908, *J. coll. Sci. Univ. Tokyo* 23 : 42.Type—*Epicephalius gracilis* Matsumura (North Africa).*Mapochia* Distant.1910, *Ins. Transvaal.* 10 : 231.Type—*Mapochia collaris* Distant (South Africa).*Mesodorydium* Melichar.1914, *Acta. Soc. ent. Bohem.* 1 : 4.Type—*Mesodorydium famelicium* Melichar (East Africa).*Paradorydium* Kirkaldy (new name for *Dorydium* Burm., 1838).1901, *Entomologist* 34 : 339.*Taxonomic Notes.*

Mapochia was referred, both by Distant and by Naudé (1926) to the LEDRINAE, and by Schumacher (1912) to the Acucephalini. Both Naudé and Haupt (1929) included *Paradorydium* in the Jassini and in 1939b I referred this genus to the EUPELICINAE.

Discussion of the HECALINAE.

The HECALINAE would appear to be a derivation from the ULOPINAE, parallel with the LEDRINAE : not only do they resemble the LEDRINAE in coloration, but there are numerous instances of superficial resemblances between representatives of the two sub-families : these resemblances are sometimes associated with secondary features in common, such as a pitted appearance and the occurrence of sparse white hairs.

APHRODINAE.

The APHRDINAE comprise small to medium-sized leaf-hoppers which are usually some shade of brown in colour, but which may also be green or black or have a yellow and black, or brown, colour pattern. The head is usually emarginate beneath the eyes and the antennal ledges are well developed and situated close to the hind margin of the face. The post-clypeus, which in most instances encroaches widely on the facial portion of the frons, frequently occupies the entire ventral surface. The frons extends on to the crown, likewise sometimes part of the frontal sutures, and postfrontal sutures are usually present : the coronal suture may be replaced by a carina, which extends on to the frons, beyond the limits of the vertex. The ocelli are dorsal in position, or marginal, and sometimes they are sunk in depressions. The tegmen may have complete venation or have supernumerary cross-veins and frequently the venation is reduced to the extent that both R_{1a} and M_{1+2} are missing. A tendency towards brachyptery exists and marked sexual dimorphism is of common occurrence. The tribes comprised in this sub-family are the Aphrodini, Errhomenellini, Evacanthini and the Signoretini.

Aphrodini (fig. 12).

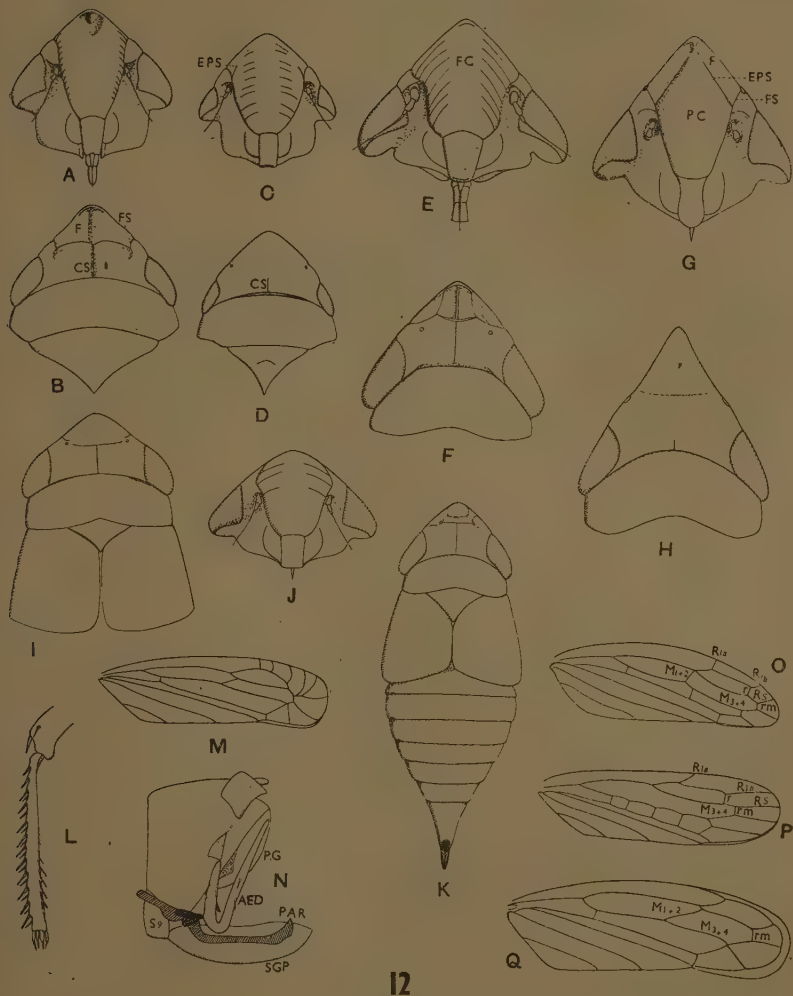


FIG. 12.

A, *Postumus hyalinus* Ev., head; B, *P. hyalinus*, head and thorax, dorsal aspect; C, *Aphrodes nervosus* Schrank, head; D, *A. nervosus*, head and thorax, dorsal aspect; E, *Euacanthella bicolor* Ev., head; F, *E. bicolor*, head and thorax, dorsal aspect; G, *Huleria quadripunctata* Ball, head; H, *Cochlorhinus phito* Uhl., head and pronotum, dorsal aspect; I, *Anoterostemma ivanoffi* Leth., head and thorax, dorsal aspect; J, *A. ivanoffi*, head; K, *Kosmiopeliv ricki* Ev.; L, *Aphrodes nervosus*, hind tibia; M, *Uhleriella signata* Ball, tegmen; N, *Aphrodes nervosus*, male genitalia; O, *Aphrodes nervosus*, tegmen; P, *Euacanthella palustris* Ev., tegmen; Q, *Postumus hyalinus*, tegmen.

Distribution.

All the principal geographical regions.

Size, Coloration and General Appearance.

The Aphrodini range in size from 4 to 8 mm. and in colour are either some shade of black, or brown, or brown with white and yellow markings. They may be flattened in shape; some are brachypterous and several exhibit pronounced sexual dimorphism, the males being smaller than the females.

Food-plants and Habits.

Aphrodes nervosus Schrank has been found feeding on Tansy (*Tanacetum vulgare*) in England (Douglas, 1889). According to Osborn (1916) *Aphrodes albifrons* L. feeds on Timothy Grass, in the United States, and the nymphs and the adults live, in large part, beneath the surface litter and in cavities in the soil around Timothy crowns. Ball (1932) is, however, of the opinion, that while *A. albifrons* is commonly found in Timothy meadows, it only feeds on plantains which grow between the Timothy clumps. Edwards (1896) records various species of *Aphrodes* as occurring at the roots of low-growing plants.

Description.

Head. The head is usually emarginate beneath the eyes and frequently arrow-shaped. The labium is short and the post-clypeus extends posteriorly as far, or nearly as far, as the hind margin of the face, and may encroach on to the crown. The maxillary plates are wide and the antennae short; the antennal ledges are likewise short, but usually distinct, and the antennal depressions are of moderate depth. The frontal region extends on to the crown, and frontal and postfrontal sutures are sometimes retained. The coronal suture is always present, but it may be replaced by a carina, which extends as far as the anterior margin of the crown. The ocelli may be either on the disk of the crown or close to, or on, its anterior margin.

Thorax. The pronotum, which is wide laterally, is sometimes slightly wider posteriorly than anteriorly, and the anterior and posterior margins are approximately parallel with each other.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are somewhat flattened, have an armature of strong spines.

Tegmina. The venation of the tegmen may be complete or reduced and additional cross-veins may be present, either in the costal region, or elsewhere.

Genera comprised in the Aphrodini.

Acocephalus Burmeister (invalid emendation of *Acucephalus* Germar).
1835, *Handbuch Ent.* 2 : 111.

Acucephalus Germar (synonym of *Aphrodes* Curtis).
1833, *Silb. Rev. Ent.* 1 : 181 (Sept.).

Type—*Cicada costata* Germar (= *Cercopis striata* Fabr., 1803 = *Cicada nervosa* Schrank, 1781) (Austria).

Anoscopus Kirschbaum (synonym of *Aphrodes* Curtis).
1858, *J. Nassau Verein für Naturk.* 13 : 357.

Type—*Anoscopus serratulae* Fabricius (Europe).

Anoterostemma Puton (invalid emendation of *Anoterostemma* Löw).
1886, *Rev. Ent.* 5 : 80 (*Cat. Hemipt. Palaearctique*).

Anoterostemma P. Löw.1885, *Verh. zool.-bot. Ges. Wien* **35** : 353.Type—*Anoterostemma henschii* Löw (= *ivanoffi* Lethierry) (S. Russia and Hungary).*Aphrodes* Curtis.1831, *Guide Brit. Ins.* (7) : 193.1833, *Ent. Mag.* **1** : 195 (Jan.).Type—*Aphrodes testuda* Curtis (= *albifrons* L.) (Britain).*Argaterma* Buchanan White.1878, *Proc. zool. Soc. Lond.* **1878** : 473.Type—*Argaterma alticola* B. White (St. Helena).*Arrugada* Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 362.Type—*Huleria rugosa* Osborn (Bolivia).*Atractotypus* Fieber (synonym of *Chiasmus* M. and R.).1866, *Verh. zool.-bot. Ges. Wien.* **16** : 501.Type—*Atractotypus bifasciatus* Fieber (Southern France).*Baileyus* Pruthi.1930, *Mem. Ind. Mus.* **11** : 31.Type—*Baileyus brunneus* Pruthi (Eastern Himalayas).*Calonia* Beamer.1940, *J. Kansas ent. Soc.* **13** : 56.Type—*Uhleriella signata* Ball (California).*Chiasmus* Mulsant and Rey.1855, *Ann. Soc. Linn. Lyon* **1855** : 215.Type—*Chiasmus translucidus* Mulsant and Rey (Southern France).*Cochlorhinus* Uhler.1876, *Bull. U.S. Geol. Survey* **1** : 358.Type—*Cochlorhinus pluto* Uhler (California).*Doratura* J. Sahlberg.1871, *Not. Sällsk. Faun. Flor. Fennica* **1871** : 291.Type—*Athysanus stylata* Boheman (Sweden).*Drionia* Osborn and Ball.1915, *Proc. biol. Soc. Wash.* **28** : 167.Type—*Drionia nigra* Ball (California).*Euacanthella* Evans.1939, *Pap. Roy. Soc. Tasm.* **1938** : 8.Type—*Euacanthella palustris* Evans (Tasmania).*Gcaleka* Naudé.1926, *S. Africa Dept. Agric. Ent. Mem.* **4** : 39.Type—*Gcaleka laticephala* Naudé (South Africa).*Gurawa* Distant.1907, *Faun. Brit. Ind. Rhyn.* **4** : 262.Type—*Gurawa vexillum* Distant (Sikkim).*Horvathiella* Matsumura.1914, *J. coll. Agric. Sapporo* **5** : 234.Type—*Horvathiella arisana* Matsumura.*Huleria* Ball.1902, *Canad. Ent.* **34** : 57.Type—*Huleria 4-punctata* Ball (California).*Kartwa* Distant (synonym of *Chiasmus* M. and R.).1908, *Faun. Brit. Ind. Rhyn.* **4** : 394.Type—*Kartwa mustelina* Distant (Calcutta).

- Kosmiopella* Kirkaldy.
1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 334.
Type—*Kosmiopella varicolor* Kirkaldy (Queensland).
- Leofa* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 86.
Type—*Leofa mysorensis* Distant (South India).
- Luheria* Osborn.
1923, *Ann. Carnegie Mus.* 15 : 31.
Type—*Luheria constricta* Osborn (Brazil).
- Memnonia* Ball.
1899, *Proc. Iowa Acad. Sci.* 7 : 66.
Type—*Memnonia consobrina* Ball (North America).
- Oniroxis* China.
1925, *Ann. Mag. nat. Hist.* (9) 16 : 484.
Type—*Oniroxis kariana* China (Yunnan).
- Penhuleria* Beamer.
1934, *Pan-Pacific Ent.* 10 : 43.
Type—*Penhuleria acuticephala* Beamer (California).
- Pholetaera* Zetterstedt (synonym of *Aphrodes* Curtis).
1840, *Ins. Lapp.* : 288.
Type—*Cercopis rustica* Fabricius (= *C. nervosa* Schrank) (Europe).
- Postumus* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 84.
Type—*Postumus facialis* Distant (South India).
- Stroggylocephalus* Flor.
1861, *Rhyn. Livlands* 2 : 210.
Type—*Stroggylocephalus agrestis* Fallen (Livland).
- Strongylocephalus* Kirschbaum (invalid emendation of *Stroggylocephalus* Flor).
1868, *Jb. Nassau Verein. Naturk.* 1868 : 73.
- Uhleriella* Ball.
1902, *Canad. Ent.* 24 : 54.
Type—*Doltocephalus coquilleti* Van Duzee (California).

Taxonomic Notes.

The distinctive features of *Aphrodes* have always received general recognition, and this genus, together with others, has in the past been placed in a group of leaf-hoppers best known as the ACUCEPHALINAE. The principal diagnostic character used in the definition of this group has been the position of the ocelli, which are situated close to the anterior margin of the crown, distant from the eyes. While some authors have included in this division genera which are in no way closely allied to *Aphrodes*, others have been of the opinion that it could not be separated from the JASSINAE (EUSCELINAE).

Edwards (1896), Melichar (1896, 1903), Lawson (1920) and Naudé (1926) all recognised the separate identity of the ACUCEPHALINAE, although the only representative of the South African fauna which Naudé referred to this sub-family actually belongs to the Ulopini (*Sichaea*).

Kirkaldy (1906), Distant (1907), Oshanin (1916), and Merino (1936) all united the ACUCEPHALINAE with the JASSINAE, while Haupt (1929) recognised the APIRODINAE and ANOTEROSTEMMINAE as separate families, later (1935) reduced to tribes. Oman (1943) places the Aphro-

dini as a tribe of the EUSCELINAE and for a group of genera, which are among those listed above, and which are confined to western North America, he has created a further tribe of the EUSCELINAE, the Cochlorhini. These genera had previously been placed by Ball (1902) in the ACOCEPHALINAE.

Errhomenellini (fig. 13).

Distribution.

Northern Europe and Western North America.

Size, Coloration and General Appearance.

The Errhomenellini range from 7 to 9 mm. in length and in colour are some shade of brown or green. They are somewhat rounded in shape and several species are brachypterous.

Food-plants and Habits.

In North America representatives of this tribe appear to be confined to the arid and semi-arid regions of the continent. *Errhomus* is restricted to the *Artemisia* belt, *Pagaronia* and *Lystridea* occur in the coastal chaparral association, while *Friscanus friscanus* Ball is apparently confined to *Lupinus arboreus* (Oman, 1938).

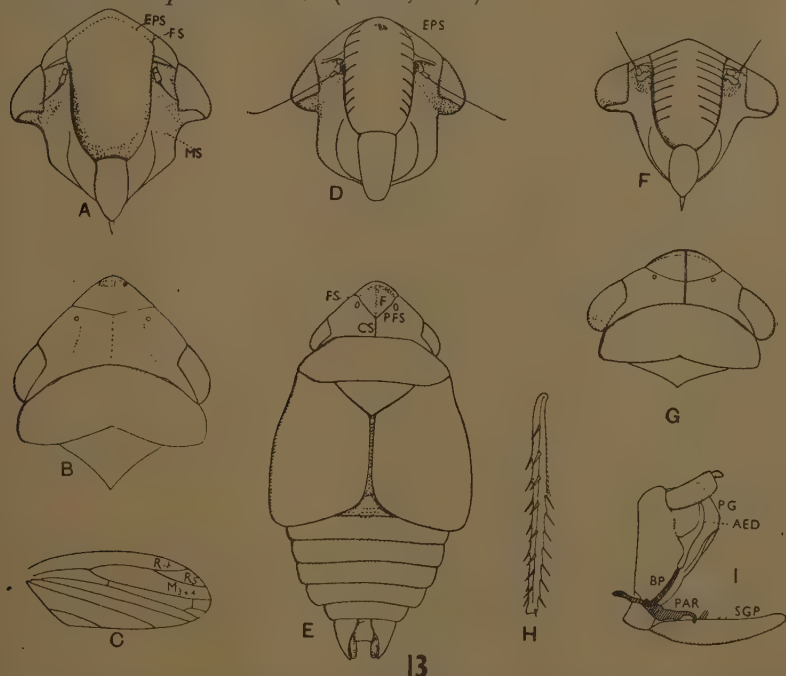


FIG. 13.

A, *Errhomus aridus* Ball, head; B, *E. aridus*, head and thorax, dorsal aspect; C, *Friscanus friscanus* Ball, tegmen; D, *Errhomenellus brachypterus* Fieb., head; E, *E. brachypterus*; F, *Lystridea uhleri* Baker, head; G, *L. uhleri*, head and thorax, dorsal aspect; H, *Friscanus friscanus*, hind tibia; I, *F. friscanus*, male genitalia.

Description.

Head. The head is emarginate beneath the eyes and the labium, of which the proximal segment may be exposed, is long or of medium length. The ante-clypeus is large and projects beyond the margin of the maxillary plates, and the post-clypeus, which is approximately parallel-sided, extends as far, or nearly as far, as the hind margin of the face. The maxillary plates may be narrow or wide and sometimes vestiges remain of the maxillary sutures. The antennae are of varying length and the antennal ledges, which are well defined, lie slightly anterior to the hind margin of the face. Such part of the frons as lies on the crown is bounded by distinct frontal and postfrontal sutures, and the coronal suture is sometimes replaced by a carina which extends on to the surface of the frons. The ocelli are on the disk of the crown.

Thorax. The pronotum, which is wide laterally, may be either parallel-sided, or wider posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded, and the hind tibiae are quadrilateral in section and bear an armature of strong spines.

Tegmina. In those forms in which the tegmen is of normal proportions both R_{1a} and M_{1+2} are usually (possibly always) absent. In others, in which the venation is reduced, the venation is obscure.

Genera comprised in the Errhomenellini.

Bathysmatophorus Sahlberg.

1871, *J. Not. Sällsk. pro Faun. et Flor. Fenn.* 9 : 109.

Type—*Bathysmatophorus reuteri* Sahlberg (Lapland).

Carsonus Oman.

1938, *Proc. U.S. nat. Mus.* 85 : 173.

Type—*Acocephalus maculatus* Gillette and Baker (North America).

Errhomenellus Puton (new name for *Errhomenus* Fieber.).

1886, *Rev. Ent.* 5 : 79 (*Cat. Hemipt. Palaearctique*).

Errhomenus Fieber (see *Errhomenellus* Puton).

1866, *Verh. zool.-bot. Ges. Wien.* 16 : 501.

Type—*Errhomenus brachypterus* Fieber (Germany).

Errhomus Oman.

1938, *Proc. U.S. nat. Mus.* 85 : 169.

Type—*Errhomenus lineatus* Baker (North America).

Friscanus Oman.

1938, *Proc. U.S. nat. Mus.* 85 : 168.

Type—*Errhomenellus friscanus* Ball (California).

Lystridea Baker.

1898, *Psyche* 1898 : 261 (*Proc. U.S. nat. Mus.* 85 : 178).

Type—*Lystridea conspersa* Baker (= *Bathysmatophorus uhleri* Baker) (North America).

Pagaronia Ball.

1902, *Canad. Ent.* 34 : 19.

Type—*Pagaronia 18-punctata* Ball (North America).

Thatuna Oman.

1938, *Proc. U.S. nat. Mus.* 85 : 176.

Type—*Thatuna gilletti* Oman (Idaho).

Taxonomic Notes.

Oshanin (1912) referred *Errhomenellus* to the Acocephalaria, while Haupt (1929) recognised the ERRHOMENELLINAE as a sub-family of the JASSIDAE. Oman, in 1938, was of the opinion that the Errhomenellini were intermediate in character between the JASSINAE and the CICADEL-

LINAE, but referred them to JASSINAE, and not to the CICADELLINAE, where they had previously been placed by Van Duzee (1917); later he changed his earlier views and included the tribe in the AMBLYCEPHALINAE (=TETTIGELLINAE) (Oman, 1943).

Evacanthini (fig. 14).

Distribution.

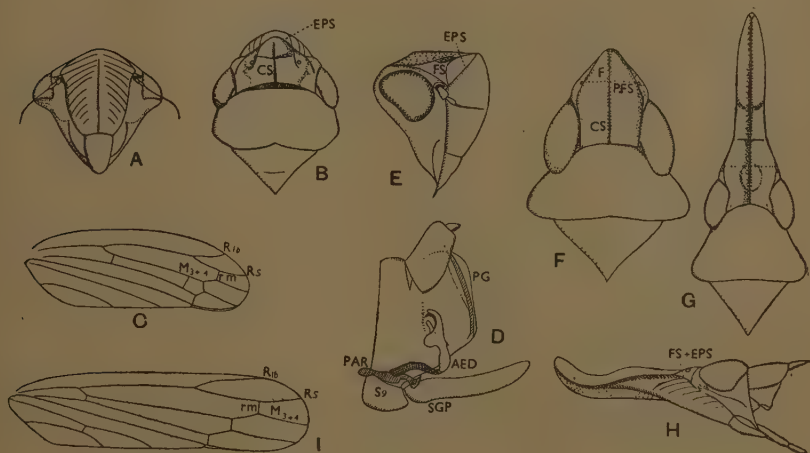
While the headquarters of this tribe would appear to be in the Oriental region, representatives occur also in Europe and in North America.

Size, Coloration and General Appearance.

The Evacanthini range in length from 4.5 to 9 mm. and in colour they are either black or brown, or one of these colours combined with yellow. In appearance they are usually cylindrical in shape, hence resemble the TETTIGELLINAE.

Food-plants and Habits.

Some species are grass-feeders, and *Evacanthus interruptus* L. has been recorded from hops (*Humulus lupulus*) in England (Masse, 1943); the same author has recorded the fact that the overwintering eggs of this species may be laid in the cracks of dead wood.



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FIG. 14.

A, *Evacanthus interruptus* L., head; B, *E. interruptus*, head and thorax, dorsal aspect; C, *E. interruptus*, tegmen; D, *Evacanthus acuminatus* Fabr., male genitalia; E, *Bundera venata*, Dist., head in lateral aspect; F, *Cunedda phaeops* Dist., head and thorax, dorsal aspect; G, *Vangama steneosaura* Dist., head and thorax, dorsal aspect; H, *V. steneosaura*, head and thorax, in profile; I, *V. steneosaura*, tegmen.

Description.

Head. The labium is short and the ante-clypeus is wide and projects beyond the margins of the maxillary plates. The maxillary plates are of varying width and vestiges may remain of the maxillary sutures. The post-clypeus, which widens posteriorly, and usually has a median carina, extends as far as the hind margin of the face, with which the epistomal suture coincides (except in a few species, where it forms a wide inverted V, fig. 14e); the post-clypeus may also become part of the crown (fig. 14b). The antennal ledges, which are short and often weak, lie close to the hind margin of the face. Such part of the frons as is not replaced by the post-clypeus is confined to the crown and the postfrontal sutures form a wide angle or a straight line. The coronal suture is replaced by a carina which extends as far, or almost as far, as the anterior margin of the crown, and there are also a pair of crinae or incomplete ridges, which extend from near the eyes and meet anteriorly in a central position. These ridges cross the frons at the junction of the frontal and postfrontal sutures and the ocelli lie lateral of them, often in depressions; these depressions are not homologous with those of the Ulopini and Stenocotini, but have been formed as a consequence of surface crumpling which has resulted from the backward development of the post-clypeus. The eyes, which are large, are depressed below the level of the crown and overlap the anterior corners of the pronotum.

Thorax. The pronotum, which is wide laterally, is usually either slightly, or else considerably, wider posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are long and flattened, are armed with well-developed spines.

Tegmina. The tegmen, which is long and narrow and has a small appendix, lacks both R_{1a} and M_{1+2} . A few species show a tendency towards a brachypterous condition.

Genera comprised in the Evacanthini.

Apphia Distant (synonym of *Onukia* Matsumura).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 4.

Type—*Apphia burmanica* Distant (Upper Burma).

Bundera Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 228.

Type—*Bundera venata* Distant (Tenasserim).

Cunedda Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 46.

Type—*Cunedda phaeops* Distant (Assam).

Dussana Distant.

1908, *Faun. Brit. Ind. Rhyn.* 4 : 322.

Type—*Dussana quaerenda* Distant (Ceylon).

Evacanthus Burmeister (invalid emendation of *Evacanthus* Lepeletier and Serville).

1835, *Handb. d. Ent.* 2 : 116.

Evacanthus Lepeletier and Serville.

1825, *Encyc. Meth.* 10 : 612.

Type—*Evacanthus interruptus* Lepeletier and Serville (France).

Mainda Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 229.

Type—*Mainda praeculta* Distant (North-West India).

Onukia Matsumura.

1912, *Annot. Zool. Japon.* 8 : 44.

Type—*Onukia onukii* Matsumura (Japan).

Pythamus Melichar.

1903, *Homopt. Faun. Ceylon* : 161.

Type—*Pythamus dealbatus* Melichar (Ceylon).

Vangama Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 260.

Type—*Vangama steneosaura* Distant (North-West India).

Taxonomic Notes.

In 1897, Osborn wrote that the position of the ocelli in *Evacanthus* suggested that this genus should be placed in the Acocephalini, even though in other respects it seemed more closely related to the TETTIGONIELLINAE. Van Duzee (1892), Edwards (1896), Melichar (1903) De Long and Caldwell (1937), and Oman (1943) have all referred *Evacanthus* to the TETTIGONIELLINAE, and Oman has created a separate tribe, the Evacanthini, to contain this genus. Haupt (1929), who recognised the EVACANTHINAE as a sub-family of the JASSIDAE, grouped within this sub-family several genera, such as *Kolla* and *Mileewa*, which I prefer to place in the TETTIGELLINAE. Baker (1923) was of the opinion that *Evacanthus* was closely related to *Signoretia* and *Pythamus*, but at the same time he created separate families for each of these genera. I have amalgamated two of Baker's families, the EVACANTHIDAE and the PYTHAMIDAE, because the genera comprised in them cannot be separated by a single significant characteristic. *Vangama*, which was referred by Distant to the GYPONINAE, Hylicaria, undoubtedly belongs to the Evacanthini.

Signoretini (fig. 15).

Distribution.

Tropical Africa and the Oriental Region.

Size, Coloration and General Appearance.

The Signoretini comprise leaf-hoppers which are about 8 mm. long, pale green in colour and pitted on the head, thorax and clavus. In shape they are long and narrow and have steeply tectiform tegmina. This tribe comprises one of the most distinctive groups of leaf-hoppers in the whole of the family JASSIDAE. According to Baker (1923), marked sexual dimorphism occurs in *Signoretia benguetensis* Baker.

Food-plants and Habits.

While specimens have frequently been swept from grasses, it is uncertain whether the Signoretini are exclusively grass-feeders.

Description.

Head. A median longitudinal carina occurs on both the face and the crown of the head. The labium is short, the ante-clypeus wide and the lora and maxillary plates are narrow. The post-clypeus, which extends as far as the posterior margin of the face, may continue on to the crown. The antennal ledges are strong and close to the hind margin of the face, and the antennal depressions are deep. The frons occupies the greater part of the crown, and the ocelli lie in depressions between the antennal ledges and the lateral carinae: the eyes, which are prominent, are depressed below the level of the crown.

Thorax. The pronotum, which has a median carina, is wide laterally and may be parallel-sided: the scutellum is small.

Legs. The tibiae are somewhat rounded and the hind tibiae have an armature of weak spines.

Tegmina. The tegmina are long and narrow and have a characteristic venation: both R_{1a} and M_{1+2} are lacking, as in the Errhomenellini and Evacanthini, but cross-vein r , which is also lacking in these two tribes, is retained in the Signoretini.

Wings. The marginal vein continues on to the anal area; this is an unusual feature which occurs also in the TARTESSUSINAE.

Male Genitalia. The male genitalia resemble those of the Errhomenellini and Evacanthini in having short parameres and dorsally directed processes on the pygophores.

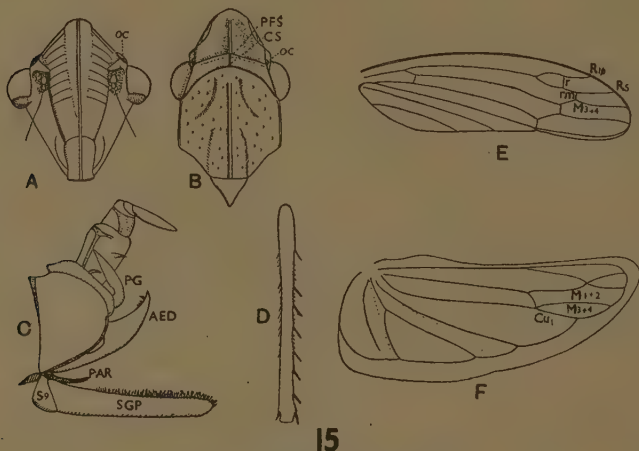


FIG. 15.—*Signoretia pacifica* Walk.

A, head; B, head and thorax, dorsal aspect; C, male genitalia; D, hind tibia; E, tegmen; F, wing.

Genera comprised in the Signoretini.

Preta Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4: 234.

Type—*Signoretia gratiosa* Melichar (Ceylon).

Signoretia Stål.

1859, *Köngl. Svensk. Eug. resa. Zool. Ins.* : 289.

Type—*Thamnotettix malaya* Stål (Malacca).

Taxonomic Notes.

Both Melichar (1903) and Distant (1907) referred *Signoretia* to the TETTIGONIELLINAE, and Baker (1915) was the first to appreciate the distinctive characteristics of this genus, for the reception of which he created a sub-family of the STENOCOTIDAE, the SIGNORETINAE; later he raised this sub-family to family status.

Discussion of the APHRODINAE.

The Aphrodini are the least specialised leaf-hoppers comprised in this sub-family, since in this tribe occur dull brown forms, somewhat ledrine in appearance, which have tegmina with complete venation and

heads lacking carinae. Next in order of descent comes the Errhomenellini, followed by the more specialised Evacanthini and Signoretini. As in the case of the LEDRINAE, it is possible to establish the relationships existing between the various tribes of the APHRODINAE, by means of a series of comparisons.

I have included the genus *Euacanthella* (fig. 12*e, f*) in the Aphrodini, though, at the time I described it, I believed it to be close to *Evacanthus*; if a comparison is made between the figures referred to above and fig. 13, it will be seen that this genus has also much in common with the Errhomenellini.

Oman (1938) has acknowledged the close relationship existing between the Evacanthini and the Errhomenellini, and the affinity between the former tribe and the Signoretini can be demonstrated by comparing fig. 14 with fig. 15.

Kirkaldy (1906) has suggested that *Aphrodes* and its allies appear to be descended from some form very near *Phrynomorphus*, but this is improbable since strong antennal ledges, which are retained in the majority of the APHRODINAE, have been lost in the EUSCELINAE.

TETTIGELLINAE.

The TETTIGELLINAE are a large group of leaf-hoppers which are allied to the APHRODINAE. The more generalised representatives are cylindrical in shape and have a head which is emarginate beneath the eyes with a swollen ante-clypeus which narrows anteriorly. The antennae are short, the antennal ledges marginal, and the post-clypeus which is swollen, but may be medially flattened, extends on to the crown. The ocelli are situated on the crown, close to the apices of the frontal sutures. The pronotum, which is wide laterally, is usually wider posteriorly than anteriorly and the tegmina, which have complete venation and a narrow appendix, are long and narrow.

There have been many and varied developments from forms such as those described above; thus the antennae may become long, the head may become produced, or flattened and shovel-shaped, and the venation of the tegmen may become reticulate. In spite of such developments the recognition of representatives of this sub-family is usually a simple matter.

The TETTIGELLINAE are usually divided into two tribes, the Tettigellini and the Proconiini. I propose to create two additional ones, the Mileewanini and the Makilingiini, the former to comprise a small group of genera which in the past have been associated with TETTIGELLA, and the latter to contain a single genus which has been referred previously to the HYLICIDAE.

Tettigellini (fig. 16*a-e, j, k*).

Distribution.

Universal, but especially well represented in tropical America.

Size, Coloration and General Appearance.

The Tettigellini range in length from 4 to 15 mm., and in colour may

be either whitish-green, or brown, or have a simple, or a complex, colour pattern in which yellow, red, and black frequently occur. They are cylindrical in shape.

Food-plants and Habits.

Several species feed on grasses and others on shrubs and trees (Kirkaldy, 1906 ; Osborn, 1929). Hackman (1922) has recorded that in the United States, *Neokolla hieroglyphica* Say has two generations which differ from each other both in feeding habits and in coloration ; the winter generation feeds on poplar and willow trees and the summer generation on ragweed (*Ambrosia trifida*).

Description.

Head. The head is approximately triangular in shape, the labium is short, the anteclypeus wide and swollen and the maxillary plates narrow or of moderate width. The postclypeus, which is considerably swollen and somewhat flattened posteriorly, extends on to the crown, where it occupies the frontal region laterally, as far as the posterior apices of the frontal sutures. A vestigial epistomal suture may be visible on the crown, but postfrontal sutures are not developed. The antennae may be either long, or short, and the antennal depressions are deep. The antennal ledges, which are situated at the hind margin of the face, are strong and rounded, but not prominent ; from above they appear as a pair of anteriorly directed lobes lying on either side of the fronto-clypeus. The ocelli, which are large, are situated on the crown, close to the apices of the frontal sutures.

Thorax. The pronotum, which is wide laterally, is either parallel-sided, or else wider posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are long and flattened, have an armature of even spines, which are either long, or of moderate length.

Tegmina. The venation of the tegmen is usually complete but in a few species additional cross-veins are present, especially in the costal area.

Wings. The venation of the wings may be reduced to the extent that R_{2+3} may be either weaker than R_{4+5} or absent altogether. In one genus (*Dilobopterus*), the anal area is distinct from the rest of the wing.

Genera comprised in the Tettigellini.

Acopsis Amyot and Serville.

1843, *Hist. Nat. Ins. Hémipt.* : 574.

Type—*Acopsis viridicans* Amyot and Serville (Isle de France).

Acrogonia Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 67.

Type—*Cicada lateralis* Fabricius (South America).

Aglena Amyot and Serville.

1843, *Hist. Nat. Ins. Hémipt.* : 575.

Type—*Jassus ornatus* Herrich Schaffer (Southern France).

Alahana Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).

Type—*Tettigoniella ericsoni* Distant (Sumatra).

Algothyma Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).

Type—*Algothyma kirschi* Melichar (Colombia).

Allocha Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).

Type—*Tettigonia sordida* Signoret (Mexico).

Allogonia Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia concinnula* Fowler (Mexico).*Amahuaka* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tettigonia angustula* Fowler (Mexico).*Amblycephalus* Curtis (preoccupied, see *Tettigella* China and Fennah).1833, *Ent. Mag.* 1 : 193 (Jan.).Type—*Cicada viridis* Linnaeus (Europe).*Amblyscarta* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 7.Type—*Cicada modesta* Fabricius (Kirkaldy, 1907) (South America).*Anchura* Melichar (preoccupied, see *Anchuralia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 344.Type—*Anchura insulta* Melichar (Peru).*Anchuralia*¹⁰ (nom. nov. pro *Anchura* Melichar (China, 1927)).*Apogonalia*¹⁰ (nom. nov. pro *Apogonia* Melichar (China, 1927)).*Apogonia* Melichar (preoccupied, see *Apogonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 344.Type—*Tettigonia stáli* Signoret (Mexico).*Apulia* Distant.1908, *Ann. Mag. nat. Hist.* (8) 1 : 525.Type—*Tettigonia quadrimacula* Walker (Colombia).*Apulina* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Apulina foveolata* Melichar (Ecuador).*Arezzia* Metcalf and Bruner.1937, *J. Agric. Univ. Porto Rico* 20 : 957.Type—*Arezzia maestralis* Metcalf and Bruner.*Aspilodora* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 346.Type—*Tettigoniella geminatula* Jacobi (Peru).*Astenogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Cicada bicolor* Fabricius (Cape of Good Hope).*Atkinsoniella* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 235.Type—*Atkinsoniella decisa* Distant (India).*Balacha* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia melanocephala* Signoret (New Grenada).*Baleja* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tettigonia flavoguttata* Latreille (Mexico).*Baramapulana* Distant.1910, *Ins. Transvaal.* 10 : 235.Type—*Baramapulana princeps* Distant (Transvaal).*Betarmonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Betarmonia puellina* Melichar (Brazil).¹⁰ Manuscript name proposed by Melichar but never published.

Bhandara Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 221.Type—*Tettigonia semiclara* Signoret (Pulo-Pinang).*Bharata* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 12.Type—*Bharata insignis* Distant (Upper Burma).*Bhooria* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 256.Type—*Bhooria modulata* Distant (Burma).*Bothrogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Cicada ferruginea* Fabricius (Oriental region, Cape of Good Hope in error).*Bucephalogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Tettigonia xanthophis* Bergoth (Argentine).*Cardioscarta* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (1931, 28 : 285).Type—*Cicada fasciata* Linnaeus (Brazil).*Carneocephala* Ball.1927, *Florida Ent.* 11 : 39.Type—*Draeculacephala floridana* Ball (Florida).*Catagonalia*¹⁰ (nom. nov. pro *Catagonia* Melichar (China, 1927)).*Catagonia* Melichar (preoccupied, see *Catagonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Tettigonia lunata* Signoret (Mexico).*Cephalogonalia*¹⁰ (nom. nov. pro *Cephalogonia* Melichar (China, 1927)).*Cephalogonia* Melichar (preoccupied, see *Cephalogonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Tettigoniella flabellula* Jacobi (Peru).*Ceratogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 350.Type—*Tettigonia recta* Fowler (Mexico).*Chromogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Chromogonia breddini* Melichar (Colombia).*Cicadella* Latreille (preoccupied, see *Tettigella* China and Fennah).1817, *Le Règne Animal* 3 : 406.Type—*Cicada viridis* Linnaeus (Van Duzee, 1917) (Europe).*Ciminius* Metcalf and Bruner.1937, *J. Agric. Porto Rico* 20 : 944.Type—*Tettigonia harti* Ball (Cuba).*Clydacha* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Phereurhinus cochlear* Jacobi (Peru).*Cofana* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Tettigonia quinquenotata* Stål (Philippines).*Conogonia* Breddin.1903, *Soc. Ent.* (Zurich) 18 : 98.Type—*Conogonia trucidula* Breddin (New Guinea).¹⁰ Manuscript name proposed by Melichar but never published.

Cyclogonia Melichar.1926—*Ann. Mus. nat. Hung.* 23 : 348.Type—*Tettigoniella cyclopula* Jacobi (Peru).*Dasmeusa* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Cicada pauperata* Fabricius (South America).*Derogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 353.Type—*Tettigonia pilipennis* Signoret (Bolivia).*Diedrocephala* Ball (see *Graphocephala* Van Duzee).1901, *Iowa Acad. Sci.* 8 : 63.Type : *Cicada coccinea* Forster (North America).*Diedrocephala* Spinola.1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 (Tavola Sinottica) : 97.Type—*Cicada variegata* Fabricius (South America).*Dilobopterus* Signoret.1850, *Rev. Mag. Zool.* 2 : 284.Type—*Dilobopterus decoratus* Signoret (= *Tettigonia dispar* Germar) (Brazil).*Draeculacephala* Ball (synonym of *Acopis* A. and S.).1901, *Proc. Iowa Acad. Sci.* 8 : 66.Type—*Tettigonia mollipes* Say (North America).*Ehagua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Ehagua polita* Melichar (Haiti).*Entogonia* Melichar (preoccupied, see *Sibovia* China).1926, *Ann. Mus. nat. Hung.* 23 : 360.Type—*Entogonia sagata* Melichar (America).*Epiacanthus* Matsumura.1902, *Termész. Füzetek.* 25 : 353.Type—*Deltocephalus stramineus* Motschulsky (Japan).*Erythrogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 373.Type—*Cicada laeta* Fabricius (Cayenne).*Eugonalia*¹⁰ (nom. nov. pro *Eugonia* Melichar (China, 1927)).*Eugonia* Melichar (preoccupied, see *Eugonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Tettigonia diversa* Signoret (Cayenne).*Eurygonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Eurygonia volturna* Melichar (Palawan).*Exogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Tettigonia assimilis* Signoret (St. Paul).*Graphocephala* Van Duzee (new name for *Diedrocephala* Ball, preoccupied).1916, *Check List Hemipt.* : 66.*Gununga* Melichar.1914, *Notes Leiden Mus.* 36 : 129 (China, 1938).Type—*Gununga jacobsoni* Melichar (Java).*Hadria* Metcalf and Bruner.1937, *J. Agric. Porto Rico* 20 : 945.Type—*Hadria convertibilis* Metcalf and Bruner (Cuba).¹⁰ Manuscript name proposed by Melichar but never published.

Helochara Fitch.1851, *Fourth Ann. Rep. State Cab. (N.Y.) Nat. Hist.* : 56.Type—*Helochara communis* Fitch (North America).*Helocharina* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tetigonia gayi* Blanchard (Chile).*Hortensia* Metcalf and Bruner.1937, *J. Agric. Univ. Porto Rico* 20 : 928.Type—*Tettigonia similis* Walker (Cuba).*Iragua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342. (China, 1938.)Type—*Iragua conjuncta* Melichar (Colombia).*Ishidaella* Matsumura.1912, *Annot. Zool. Japon.* 8 : 41.Type—*Tettigonia albomarginata* Signoret (New Holland) (China and Fennah, 1946).*Juliaca* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Juliaca ujhelyii* Melichar (Colombia).*Kikuchiella* Kato.1932, *Kontyu* 5 : 223.Type—*Kikuchiella gracilis* Kato.*Kolla* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 223.Type—*Kolla insignis* Distant (India).*Lucumius* Metcalf and Bruner.1937, *J. Agric. Univ. Porto Rico* 20 : 968.Type—*Lucumius triangularis* Metcalf and Bruner (Cuba).*Luzoniella* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Luzoniella philippina* Melichar (Philippines).*Maguangua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Maguangua biroï* Melichar (New Guinea).*Mareja* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia limbaticollis* Stål (Mexico).*Mesogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia ferratula* Breddin (Ecuador).*Metascarta* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia flavipes* Signoret (Bolivia).*Microgoniella* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Cicada pudica* Fabricius (South America).*Murata* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Murata obscura* Melichar (New Guinea).*Neokolla* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia hieroglyphica* Say (North America).

Onega Distant.1908, *Ann. Mag. nat. Hist.* (8) 1 : 528.Type—*Onega avella* Distant (Ecuador).*Oragua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tettigonia nebulosa* Signoret (Brazil).*Orechona* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344.Type—*Orechona trifoveolata* Melichar (Ecuador).*Orectogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Tettigonia sparsula* Signoret (Brazil).*Oxycoryphia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tettigonia spatulato* Signoret (New Grenada).✓ *Oxygonalia*¹⁰ (nom. nov. pro *Oxygonia* Melichar (China, 1927)).*Oxygonia* Melichar (preoccupied, see *Oxygonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Ciccus ignifer* Walker (Colombia).*Pachitea* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigoniella habenula* Jacobi (Peru).*Pamplona* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tettigonia feralis* Fowler (Panama).*Pañacatua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 340.Type—*Tettigonia rubrolimbata* Signoret (Bolivia).✓ *Paragonalia*¹⁰ (nom. nov. pro *Paragonia* Melichar (China, 1927)).*Paragonia* Melichar (preoccupied, see *Paragonalia* Evans).1926, *Ann. Mus. nat. Hung.* 23 : 342. (China, 1938).Type—*Tettigonia sanguinicolis* Latreille, 1812 (Colombia).*Parinaeota* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Parinaeota bakeri* Melichar (Peru).*Paromenia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 342 (China, 1938).Type—*Tettigonia rufa* Walker (Venezuela).*Phereurhinus* Jacobi.1905, *Sitz. Ber. Ges. Naturf. Berlin* 1905 : 168.Type—*Phereurhinus batillus* Jacobi (Peru).*Pherodes* Fowler.1899, *Biol. Centr. Amer. Rhyn. Homopt.* 2 : 225.Type—*Pherodes flammeicolor* Fowler (Mexico).*Pisacha* Distant (preoccupied, see *Pisachoides* Distant).1907, *Faun. Brit. Ind. Rhyn.* 4 : 230.Type—*Pisacha primitiva* Distant (Burma).*Pisachoides* Distant (new name for *Pisacha* Distant).1918, *Faun. Brit. Ind. Rhyn.* 7 : 12.*Plesiommata* Provancher.1889, *Pet. Faune Ent. Canada* 3 : 263.Type—*Plesiommata biundulata* Provancher (Canada).¹⁰ Manuscript name proposed by Melichar but never published.

Poeciloscarta Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 73.Type—*Cicada cardinalis* Fabricius (Distant, 1908) (South America).*Polisanella* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Polisanella bakeri* Melichar (Philippines).*Poochara* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 77.Type—*Cicada farinosa* Fabricius (Sumatra).*Pseudoscarta* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Cicada fastuosa* Fabricius (South America).*Rhopalogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 341 (China, 1938).Type—*Tettigonia scita* Walker (Venezuela).*Santarema* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Santarema acocephala* Melichar (Peru).*Serpa* Distant.1908, *Ann. Mag. nat. Hist.* (8) 1 : 529.Type—*Tettigonia plumbea* Walker (Ecuador).*Sibovia* China (new name for *Entogonia* Melichar).1927, *Ann. Mag. nat. Hist.* (9) 20 : 283.*Soibanga* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 236.Type—*Tettigonia bella* Walker (Northern India).*Sphinctogonia* Breddin.1901, *Abh. Natur. Ges. Halle* 24 : 128.Type—*Sphinctogonia quincunula* Breddin (= *Tettigonia guttivitta* Walker. (Melichar, 1926)) (North Celebes).*Strictogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 358.Type—*Cicada unifasciata* Fabricius (South America).*Synogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tettigonia nasuta* Fowler (Guatemala).*Tacora* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 359.Type—*Tettigonia dilecta* Walker (South America).*Tahura* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 343 (China, 1938).Type—*Tahura fowleri* Melichar (Peru).*Tettigella* China and Fennah (new name for *Tetigonia* auctt. nec Geoff. ;*Tettigonia* auctt., nec L. and *Tettigoniella* auctt., nec Jac.).1946, *Ann. Mag. nat. Hist.* (11) 12, 1945 : 711.Type—*Cicadella viridis* Linnaeus (Europe).*Tipuana* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 344 (China, 1938).Type—*Tipuana egregia* Melichar (Bolivia).*Tylozygus* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 501.Type—*Tettigonia nigrolineata* Herrich Schaffer (Bohemia).

Ulozena Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 345 (China, 1938).Type—*Tettigonia lineatocollis* Signoret (Madagascar).*Wutingia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 372.Type—*Wutingia nigronevosa* Melichar (China).*Zaruma* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 347.Type—*Zaruma vexata* Melichar (Ecuador).*Taxonomic Notes.*

While this group of leaf-hoppers, which has at various times been referred to as the CICADELLINAE, TETIGONIINAE, Tettigonini, TETTIGONIELLIDAE and AMBLYCEPHALINAE, has always been recognised as a distinct division of the JASSIDAE, opinions have differed as to its components. Melichar (1903) referred *Signoretia*, *Pythamus* and *Penthimia* to the Tettigonini and Distant (1908) did likewise with the first two of these genera. Baker (1915) placed *Hylica*, *Gypona*, *Penthimia* and *Errhomenellus* with *Tettigoniella* in the TETTIGONIELLIDAE, and Oman (1943) has divided the AMBLYCEPHALINAE into the Amblycephalini, Proconiini, Errhomenellini and Evacanthini. While I agree that, with the exception of *Hylica*, *Penthimia* and *Gypona*, the various other genera referred to above are not far removed from *Tettigella*, I am of the opinion that their true inter-relationships are best indicated if they are referred to a separate sub-family.

Bhooria, which was placed by Distant in the Hyliciaria, certainly belongs to the Tettigellini, but *Aglena*, which was referred by Melichar (1896) to the Tettigonini and by Baker (1915) to the JASSINAE, is only tentatively included in this tribe.

Proconiini (fig. 16, *h*, *i*, *l-o*, *s.*)*Distribution.*

Neartic, Neotropical and Oriental regions.

Size, Coloration and General Appearance.

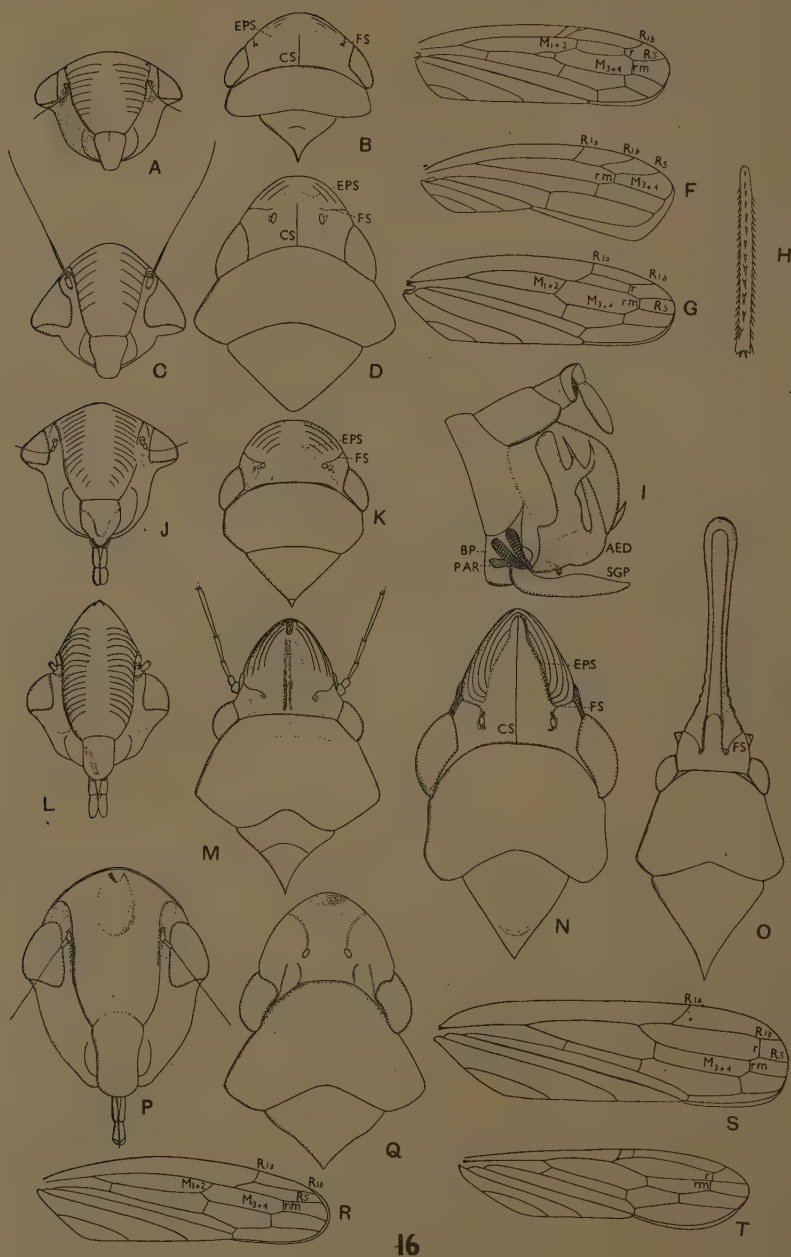
The Proconiini range in length from 10 to 22 mm. and in colour they are usually some shade of black, grey, brown, or white, often with yellow markings: a few species are green or red. The majority are large, cylindrically-shaped insects with a bulbous face and several have a bizarre appearance.

Food-plants and Habits.

The food-plants, as in the Tettigellini, are of a varied nature.

Description.

Head. The head may be widely or narrowly produced, the labium is short and the anteclypeus swollen. The post-clypeus is swollen and sometimes flattened posteriorly; it may lie in three planes, of which the middle plane is at right-angles to the axis of the body, and it extends on to the crown, where it completely replaces the frons. The antennae are long, and that part of the antenna nearest to the base may be divided into several distinct



segments. The antennal ledges, which are prominent and form a bridge linking the eyes with the post-clypeus (which they overlap), appear from above as a pair of finger-like lobes. The antennal depressions are deep, and the ocelli, which are situated on the crown, are often raised on prominences. The crown is extensive, and frequently has a median longitudinal groove, and the eyes are prominent.

Thorax. The pronotum, which may be rugose, is sometimes parallel-sided, but more usually is wider posteriorly than anteriorly; sometimes it is declivous and it may have a median longitudinal keel, or lateral prominences.

Legs. The fore tibiae are usually quadrilateral in section and apically thickened with a groove along the exterior surface, but they may be flattened or even foliaceous. The middle and hind tibiae are quadrilateral in section and the latter bear small, even spines.

Tegmina. The tegmina, which may be coriaceous or transparent, usually have complete venation, but sometimes the venation is reticulate. The proximal cross-vein between R_3 and M may be situated distad of $m-cu_2$, and M may be fused with R to as far almost as the point where R_3 arises.

Genera comprised in the Proconiini.

Abana Distant.

1908, *Ann. Mag. nat. Hist.* (8), 22 : 72.

Type—*Aulacizes dives* Walker (Ecuador).

Acharista Melichar.

1925, *Ann. Mus. nat. Hung.* 22 : 368.

Type—*Acharista variolata* Melichar (Bolivia).

Acrobelus Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 60.

Type—*Tettigonia reflexa* Signoret (West Coast of America).

Acrocampsia Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 66.

Type—*Fulgora pallipes* Fabricius (Cayenne).

Aguana Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 280.

Type—*Tettigonia imbricata* Signoret (Brazil).

Amalfia Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 281.

Type—*Scaris latipennis* Walker (= *Tettigonia latipennis* Signoret) (Bolivia).

Amblydisca Stål.

1869, *Köngl. Svensk. Vet.-Akad. Handl.* 8 : 61.

Type—*Tettigonia rubriventris* Signoret (Mexico).

Andamaroa Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 336.

Type—*Tettigonia physiocephala* Signoret.

FIG. 16.

A, *Aglena ornata* H.S., head; B, *A. ornata*, head and thorax, dorsal aspect; C, *Mileewa margherita* Dist., head; D, *M. margherita*, head and thorax, dorsal aspect; E, *Aglena ornata*, tegmen; F, *Mileewa margherita*, tegmen; G, *Tettigella viridis* L., tegmen; H, *Oncometopia undata* Fabr., hind tibia; I, *O. undata*, male genitalia; J, *Tettigella viridis*, head; K, *T. viridis*, head and thorax, dorsal aspect; L, *Ciccus latreilli* Dist., head; M, *C. latreilli*, head and thorax, dorsal aspect; N, *Phera unipunctata* Ev., head and thorax, dorsal aspect; O, *Namsangia garialis* Dist., head and thorax, dorsal aspect; P, *Makilingia nigra* Baker, head; Q, *M. nigra*, head and thorax, dorsal aspect; R, *M. nigra*, tegmen; S, *Ciccus latreilli*, tegmen; T, *Phera unipunctata*, tegmen.

Aulacizes Amyot and Serville.

1843, *Hist. Nat. ins. Hémipt.* : 571.

Type—*Tettigonia quadripunctata* Germar (Brazil).

Backhoffella Schmidt.

1928, *Wien. ent. Ztg.* 45 : 83.

Type—*Backhoffella pulchra* Schmidt (Peru).

Campecha Melichar.

1925, *Ann. Mus. nat. Hung.* 23 : 363.

Type—*Tettigonia semirasa* Fowler (Mexico).

Capinota Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 319.

Type—*Capinota fowleri* Melichar (Mexico).

Caripuna Melichar.

1926, *Ann. Mus. nat. Hung.* 23 : 318.

Type—*Tettigonia guerini* Signoret (Cayenne).

Catorthorrhinus Fowler.

1898, *Biol. Centr. Amer. Hom.* 11 : 213.

Type—*Catorthorrhinus resimus* Fowler (Panama).

Caxia Melichar.

1925, *Ann. Mus. nat. Hung.* 22 : 358.

Type—*Caxia projecta* Melichar (New Guinea).

Centrometopia Melichar (preoccupied, see *Molomea* China).

1925, *Ann. Mus. nat. Hung.* 22 : 370.

Type—*Tettigonia personata* Signoret (Brazil).

Centrometopoides Strand (new name for *Centrometopia* Melichar, invalid).

1928, *Arch. Naturges.* 92 (A) 8 : 73.

Chiapusa Schmidt.

1928, *Stettin. ent. Zeit.* 89 : 40.

Type—*Tettigonia rugicollis* Signoret (Mexico).

Ciccus Latreille.

1829, *Cuvier's Règne Animal*, ed. 2, 5 : 221.

Type—*Cicada adspersa* Latreille et auctt., nec Fabricius = *Ciccus latreilli*

Distant, nom. nov. (Distant, 1908) (Brazil).

Coelopola Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 65.

Type—*Cicada adspersa* Fabricius (Distant, 1908) (South America).

Cuerna Melichar.

1925, *Ann. Mus. nat. Hung.* 22 : 363.

Type—*Cercopis lateralis* Fabricius, 1798 (Carolina).

Cymbalopus Kirkaldy (synonym of *Peltocheirus* Walker).

1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 88.

Type—*Tettigonia bigibbosus* Signoret (Cayenne).

Cyrtodisca Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 60.

Type—*Tettigonia major* Signoret (Guatemala).

Dichometopia Melichar (preoccupied, see *Egidemia* China).

1925, *Ann. Mus. nat. Hung.* 22 : 370.

Type—*Oncometopia anceps* Fowler (Central America).

Dichrophleps Stål.

1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 62.

Type—*Cicada aurea* Fabricius (South America).

Dictyodisca Schmidt.

1928, *Stettin. ent. Zeit.* 89 : 50.

Type—*Amblydisca salvini* Fowler (Panama).

- Diestostemma* Amyot and Serville.
1843, *Hist. Nat. Ins. Hémipt.* ; 572.
Type—*Cicada albipennis* Fabricius (South America).
- Ectypus* Signoret.
1853, *Rev. Mag. Zool.* 5 : 263.
Type—*Ectypus coriaceus* Signoret (Bolivia).
- Egidemia* China (new name for *Dichometopia* Melichar).
1927, *Ann. Mag. nat. Hist.* (9) 20 : 283.
- Eustollia* Goding (synonym of *Proconia* Lepeletier and Serville).
1926, *Trans. Amer. ent. Soc.*, 52 : 105.
Type—*Cicada jubata* Goding (= *C. cucullata* Laporte) (Surinam).
- Gernaria* Laporte (synonym of *Proconia* Lepeletier and Serville).
1832, *Ann. Soc. ent. Fr.* 1 : 222.
Type—*Gernaria cucullata* Laporte (= *C. marmorata* Fabricius) (Cayenne).
- Heterometopia* Melichar (preoccupied, see *Hyogonia*, China).
1925, *Ann. Mus. nat. Hung.* 22 : 370.
Type—*Heterometopia reticulata* Melichar (South America).
- Heterostemma* Melichar.
1924, *Ann. Mus. nat. Hung.* 21 : 227.
Type—*Tettigonia nervosa* Signoret (Colombia).
- Homalodisca* Stål.
1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 63.
Type—*Cicada triquetra* Fabricius (Distant, 1908) (South America).
- Homalogoniella* Melichar.
1925, *Ann. Mus. nat. Hung.* 22 : 341.
Type—*Tettigonia pubescens* Signoret (Brazil ?).
- Homoscarta* Melichar.
1926, *Ann. Mus. nat. Hung.* 23 : 278.
Type—*Tettigonia irregularis* Signoret (Bolivia).
- Hyogonia* China (new name for *Heterometopia* Melichar).
1927, *Ann. Mag. nat. Hist.* (9) 20 : 283.
- Ichthyobelus* Melichar.
1925, *Ann. Mus. nat. Hung.* 22 : 360.
Type—*Ichthyobelus bellicosus* Melichar (Peru).
- Jilijapa* Melichar.
1925, *Ann. Mus. nat. Hung.* 22 : 356.
Type—*Jilijapa armata* Melichar (Cochin China).
- Lebora* China (new name for *Parametopia* Melichar).
1927, *Ann. Mag. nat. Hist.* (9) 20 : 283.
- Leucopepla* Kirkaldy.
1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 87.
Type—*Tettigonia bituberculata* Signoret (Brazil).
- Lissocarta* Stål.
1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 69.
Type—*Cicada vespiformis* Fabricius (South America).
- Logata* Strand (new name for *Lova* Schmidt).
1933, *Folia zool. hydrobiol.* 5 : 122.
- Lova* Schmidt.
1932, *Wien. ent. Ztg.* 49 : 47.
Type—*Lova ohausi* Schmidt (Ecuador).
- Mareba* Distant.
1908, *Ann. Mag. nat. Hist.* (8) 11 : 77.
Type—*Mareba eresia* Distant (Ecuador).

Marizella Schmidt.1928, *Wien. ent. Ztg.* 45 : 82.Type—*Marizella polita* Schmidt (Ecuador).*Molomea* China (new name for *Centrometopea* Melichar).1927, *Ann. Mag. nat. Hist.* (9) 20 : 283.*Mucrometopia* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 370.Type—*Tettigonia caudata* Walker (Bolivia).*Myogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 332.Type—*Tettigonia limpida* Signoret (Brazil).*Namsangia* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 259.Type—*Namsangia garialis* Distant (Assam).*Neiva* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 368.Type—*Neiva rufipes* Melichar (Ecuador).*Ochrostacta* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 61.Type—*Tettigonia diadema* Burmeister (Kirkaldy, 1907) (Montevideo).*Omagua* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 350.Type—*Tettigonia fitchii* Signoret (Cayenne).*Oncometopia* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 62.Type—*Cicada undata* Fabricius (Distant, 1908) (Carolina).*Ortega* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 280.Type—*Tettigonia truncatipennis* Signoret (= *Scaris obliqua* Walker) (Bolivia).*Papallacta* Schmidt.1932, *Wien. ent. Ztg.* 49 : 47.Type—*Papallacta haenschi* Schmidt (Ecuador).*Parametopia* Melichar (see *Lebora*, China).1925, *Ann. Mus. nat. Hung.* 22 : 370.Type—*Cicada orbona* Fabricius (Brazil).*Parathona* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 330.Type—*Cicada lyncea* Fabricius (India).*Peltocheirus* Walker.1858, *List Homopt. Brit. Mus. Suppl.* : 247.Type—*Tettigonia bigibbosus* Signoret (Cayenne).*Phera* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 60.Type—*Tettigonia centrolineata* Signoret (Mexico).*Pibrochoides* Haupt (synonym of *Chiapusia* Schmidt).1929, *Zool. Jb.* 58 : 252.Type—*Tettigonia rugicollis* Signoret (Mexico).*Platygonia* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 340.Type—*Tettigonia praestantior* Fowler (Panama).

Proconia Lepeletier and Serville.1828, *Encyc. Méth.* 10 : 610.Type—*Cicada cristata* Fabricius (= *C. marmorata* Fabricius, Distant, 1908) (South America).*Propetes* Walker.1851, *List Homopt. Brit. Mus.* 3 : 797.Type—*Propetes compressa* Walker (Brazil).*Pseudometopia* Schmidt.1928, *Wien. ent. Ztg.* 45 : 74.Type—*Pseudometopia appendiculata* Schmidt (Colombia).*Pseudophera* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 332.Type—*Proconia atra* Walker (Honduras).*Raphirhinus* Laporte.1832, *Ann. Soc. ent. Fr.* 1 : 413.Type—*Fulgora adscendens* Fabricius (= *F. phosphorea*, Melichar, 1925) (Cayenne).*Rhaphidorhinus* Stål (invalid emendation of *Raphirhinus* Laporte).1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 60, 62.*Rhaphirhinus* Amyot and Serville (invalid emendation of *Raphirhinus* Laporte).1843, *Hist. Nat. Ins.* : 573.*Sphaeropogonia* Breddin.1901, *Soc. Ent.* 16 : 100.Type—*Sphaeropogonia aureatula* Breddin (Melichar, 1926) (Ecuador).*Splonia* Signoret.1891, *Ann. Soc. ent. Fr.* 60 : 467.Type—*Splonia acutalis* Signoret (Senegal).*Stictoscarta* Stål.1869, *K. Svensk. Vet.-Akad. Handl.* 8 : 61.Type—*Tettigonia sulcicollis* Germar (Distant, 1908) (Brazil).*Syringophora* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 87.Type—*Tettigonia brevis* Walker (China).*Tapajosa* Melichar.1924, *Ann. Mus. nat. Hung.* 21 : 241.Type—*Tettigonia fulvopunctata* Signoret (Brazil).*Teleogonia* Melichar.1925, *Ann. Mus. nat. Hung.* 22 : 361.Type—*Tettigonia fusca* Walker (Colombia).*Teletusa* Distant.1908, *Ann. Mag. nat. Hist.* (8) 11 : 78.Type—*Teletusa paraguayensis* Distant (Paraguay).*Tolua* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 298.Type—*Aulacizes multiguttata* Stål (Mexico).*Tretogonia* Melichar.1926, *Ann. Mus. nat. Hung.* 23 : 273.Type—*Tettigonia pruinosa* Walker (Brazil).*Trichogonia* Breddin.1901, *Soc. Ent.* 16 : 75.Type—*Trichogonia ardentula* Breddin (Ecuador).

- Williamsiana* Goding (synonym of *Zyzzogeton* Breddin).
 1926, *Trans. Amer. ent. Soc.* **52** : 103.
 Type—*Williamsiana ferruginosa* Goding (Ecuador).
Yotala Melichar.
 1925, *Ann. Mus. nat. Hung.* **22** : 336.
 Type—*Yotala boliviana* Melichar (Bolivia).
Yunga Melichar.
 1924, *Ann. Mus. nat. Hung.* **21** : 208.
 Type—*Aulacizes coriacea* Stål. (Mexico).
Zyzza Kirkaldy (new name for *Germaria* Laporte).
 1900, *Entomologist* **33** : 243.
Zyzzogeton Breddin.
 1902, *Soc. Ent.* **16** : 178.
 Type—*Zyzzogeton haenschi* Breddin (Ecuador).

Taxonomic Notes.

Namsangia, which was placed by Distant in the GYPONINAE, Hyliaria, belongs undoubtedly to the TETTIGELLINAE, but its inclusion within the Proconiini must be regarded as provisional.

Mileewanini (fig. 16, c, d, f).

Distribution.

Southern and Tropical Africa and the Oriental region.

Size, Coloration and General Appearance.

Leaf-hoppers comprised in this tribe are approximately 5 mm. long, and in colour they are either dark brown, or black, with restricted hyaline areas on the tegmen; they have a fragile appearance and are not cylindrical in shape.

Food-plants and Habits.

Apparently unknown.

Description.

Head. The labium is of moderate length, the ante-clypeus swollen, and the transverse suture, which separates the ante-clypeus from the post-clypeus, is indistinct; the post-clypeus, which is medially flattened and laterally swollen, extends on to the crown. No trace remains of a separate frons and even the frontal sutures may be vestigial. The antennae are long, the antennal depressions shallow, and the antennal ledges, which are obscure, form part of the curve of the hind margin of the face. The ocelli are situated on the crown.

Thorax. The pronotum, which is wide laterally, broadens posteriorly.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are somewhat flattened, have an armature of long, slender spines.

Tegmina. The clavus is small and the tegmen is apically blunt due to the occurrence of a large appendix and a large cubital cell: M_{1+2} is absent and only a single cross-vein occurs between M and Cu_1 .

Genera comprised in the Mileewanini.

Augulus Distant (synonym of *Mileewa* Distant).

1918, *Faun. Brit. Ind. Rhyn.* **7** : 98.

Type—*Augulus typicus* Distant (Assam).

Bolinlila Distant (synonym of *Mileewa* Distant).

1910, *Ins. Transvaal*. 10 : 234.

Type—*Bolinlila rhodesiana* Distant (East Africa).

Faenius Distant (synonym of *Mileewa* Distant).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 14.

Type—*Faenius lynchi* Distant (Northern India).

Mileewa Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 238.

Type—*Mileewa margherita* Distant (Assam).

Tylozygoides Matsumura (synonym of *Mileewa* Distant).

1912, *Annot. Zool. Japon.* 8 : 42.

Type—*Tylozygoides artemesiae* Matsumura (Formosa).

Ujna Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 239.

Type—*Ujna delicatula* Distant (Ceylon).

Taxonomic Notes.

With the exception of *Augulus*, which Distant referred to the TYPHLOCYBINAE, the above genera have previously been included in the TETTIGELLINAE. In a few species comprised in other genera the venation of the tegmen is similar to that of *Mileewa* (e.g., *Diedrocephala angustula* Fowler), but such species lack the characteristic appearance of *Mileewa* and related genera.

Makilingiini (fig. 16, p-r).

Distribution.

Philippine Islands.

Size, Coloration and General Appearance.

Makilingia nigra Baker (♀) is 6 mm. long, and *Makilingia* spp. are black, black and red, or whitish (Merino, 1936). In appearance these insects are dorsally flattened with steeply tectiform tegmina, and have the head, thorax, and tegmina punctate. According to Baker (1924) marked sexual dimorphism occurs, especially shown in the shape of the head.

Food-plants and Habits.

Makilingia spp. are essentially forest insects (Baker, 1914).

Description.¹¹

Head. The labium is short, the ante-clypeus is wide and slightly convex, and the transverse suture which separates the ante-clypeus from the post-clypeus is obscure. The post-clypeus is medially flat, laterally rounded, and posteriorly depressed, and the lora are small and the maxillary plates wide. The antennae are of medium length; the antennal depressions are shallow, and the antennal ledges, which extend between the fronto-clypeus and the eyes, form a narrow curved posterior boundary to the sides of the face. The crown, which is widely curved anteriorly, overlaps the eyes laterally. The apical border of the crown is narrow and carinate, and posterior to this border the crown is flattened and depressed; the ocelli are situated on the crown.

Thorax. The pronotum is wide laterally and broadest posteriorly.

¹¹ Based on a single specimen of *M. nigra*.

Legs. The anterior tibiae are rounded and the hind tibiae, which are somewhat flattened, are armed with even spines of moderate length.

Tegmina. The tegmina, which are long and narrow, have complete venation.

Genera comprised in the Makilingiini.

Makilingia Baker.

1914, *Philipp. J. Sci.* 9 : 409.

Type—*Makilingia nigra* Baker (Philippines).

Taxonomic Notes.

Baker originally believed that *Makilingia* was related to genera comprised in the HYLICINAE, especially to *Bhooria* (which actually belongs to the TETTIGELLINAE); later (1924) he referred the genus to the SUDRINAE, GYPONIDAE. Merino (1926), who placed *Makilingia* in the TETTIGONIELLIDAE, considered that *Tettigoniella* (*Tettigella*) occupied an intermediate position between *Gypona* and *Makilingia*.

Even although in superficial features the head of *M. nigra* differs widely from those of *Tettigella* spp., in basic structure the heads of species belonging to these two genera are very similar: likewise the shape and venation of the tegmen of *M. nigra* is similar to those of *Tettigella* spp. For these reasons I have no hesitation in referring *Makilingia* to the TETTIGELLINAE, its distinctive features being recognised by the creation of a tribe for its sole reception.

Discussion of the TETTIGELLINAE.

This sub-family, which is essentially an American group of leaf-hoppers, although now of world-wide distribution, represents the culmination of the development of the Ulopides. While Spooner (1938) has suggested that the TETTIGELLINAE are of separate derivation from the rest of the JASSIDAE (because he was of the opinion that the possession of a swollen post-clypeus implied relationship with the CERCOPIDAE), it is more probable that they have been derived from an Aphrodine stem, and are a development parallel to the Errhomenellini, Signoretini and Evacanthini.

A few species occur in countries with cool climates: some even are sub-alpine insects, but the greater number lives in, or near, the tropics of the New World.

NIRVANINAE (fig. 17).

Baker (1923) divided the NIRVANIDAE into three sub-families, the NIRVANIINAE, MACROCERATOGONIINAE and the STENOMETOPIINAE; but I am unable to adopt the same procedure, since I have seen specimens of neither *Macroceratogonia* nor *Stenometopius*. Further study of this sub-family will undoubtedly result in its subdivision into several tribes, but meanwhile it is best regarded as a single unit.

Distribution.

The headquarters of the NIRVANINAE would appear to be in the Oriental region, but representatives also occur in Southern and Tropical Africa, Australia, South America and Costa Rica.

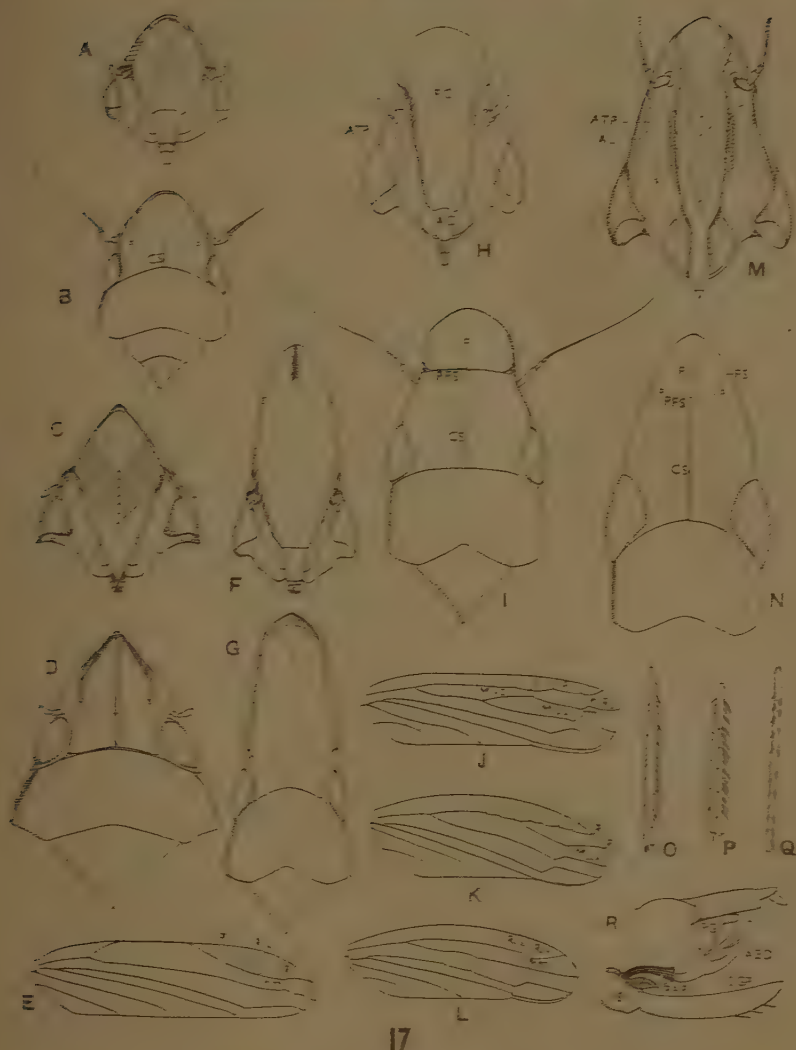


FIG. 17.

- A. *Kana dorsigenis* Ev., head; B. *K. dorsigenis*, head and thorax, dorsal aspect; C. *Scutotoma incarpit* Baker, head; D. *S. incarpit*, head and thorax, dorsal aspect; E. *Holodromus typicus* Dist., tegmen; F. *H. typicus*, head; G. *H. typicus*, head and thorax, dorsal aspect; H. *Chlorotus typicus* Dist., head; I. *O. typicus*, head and thorax, dorsal aspect; J. *Phanerothrips typicus* Ev., tegmen; K. *Scutotoma incarpit*, tegmen; L. *Scutotoma incarpit* Ev., tegmen; M. *Chlorotus typicus*, head; N. *O. typicus*, head and thorax, dorsal aspect; O. *Holodromus typicus*, hind genitalia; P. *Chlorotus typicus*, hind tibia; Q. *Chlorotus typicus*, hind tibia; R. *Audromorpha*, male genitalia.

Size, Coloration and General Appearance.

The NIRVANINAE range from 5 to 9 mm. in length and in colour are usually yellow, white, or orange with, or without, red or dark markings. In appearance they are somewhat flattened, and have long antennae and obscure tegminal venation: marked sexual dimorphism occurs in some genera.

Food-plants and Habits.

Nirvana pallida Melichar and *N. suturalis* Melichar have been recorded as destructive to sugar-cane and grasses in Formosa (Schumacher, 1915); *Stenotortor inocarpi* Baker as feeding on LEGUMINOSAE at Singapore (Baker, 1923) and *Occinirvana eborea* Evans has been taken on *Casuarina* in Western Australia.

Description.

Head. The labium, which is occasionally of moderate length, is usually very short, and the ante-clypeus, which is either swollen or flat, is sometimes separated from the post-clypeus by a transverse suture. The lora are frequently small, and the maxillary plates are of varying width. The post-clypeus, which sometimes has a median carina, is either concave or flat, and extends posteriorly as far as the hind margin of the face; apically the face is either narrowly carinate, or broad and flat, or concave, and the attachments of the cibarial muscles may be visible on a wide margin which separates the face from the crown. The antennae are very long, the antennal depressions deep, and the antennal ledges, which are usually prominent, are either transverse, or the lateral apices may be directed towards the eyes. In those forms in which the head is produced, the antennal depressions are shallow, and the antennal ledges may be obscure, or they may become part of the recurved borders of the sides of the face. Although any trace of a separate frons is seldom retained on the face of the head, the frons may remain well defined on the crown, and the ocelli, which are on the crown, are laterally placed in the neighbourhood of the antennae. The eyes may be depressed below the level of the crown.

Thorax. The pronotum, which is wide laterally, may either be collar-like, or wider posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded; the hind tibiae are variable in shape, length, and strength, and also in the nature of their armature of spines.

Tegmina. The venation of the tegmen is occasionally complete but for cross-vein $m-cu_2$, which is invariably absent; but it is usually reduced to the extent that M_{1+2} is lacking. In several species additional costal veinlets are developed, and the venation is frequently obscure.

Genera comprised in the NIRVANINAE.

Atritona Melichar.

1914, *Acta. Soc. ent. Bohem.* 11 : 5.

Type—*Atritona paradoxa* Melichar (East Africa).

Austronirvana Evans.

1941, *Trans. Roy. Soc. S. Aust.* 63 : 41.

Type—*Austronirvana flava* Evans (Queensland).

Balbillus Distant.

1908, *Faun. Brit. Ind. Rhyn.* 4 : 287.

Type—*Balbillus granulosus* Distant (Ceylon).

Buloria Distant.

1908, *Faun. Brit. Ind. Rhyn.* 4 : 271.

Type—*Buloria gyponinoides* Distant (India).

Carchariacephalus Montrouzier.1861, *Ann. Soc. ent. Fr.* (4) 1 : 71.Type—*Carchariacephalus forestieri* Montrouzier (New Caledonia).*Chudania* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 268.Type—*Chudania delecta* Distant (North India).*Crispina* Distant.1918, *Faun. Brit. India. Rhyn.* 7 : 76.Type—*Crispina nigristigma* Distant (South India).*Didius* Distant (synonym of *Omaranus* Distant).1918, *Faun. Brit. Ind. Rhyn.* 7 : 36.Type—*Didius sexualis* Distant (Bengal).*Hodoedoecus* Jacobi.1910, *Sjöstedts Kilimandjaro Meru Exp.* 12 : 126.Type—*Hodoedoecus acuminifrons* Jacobi (East Africa).*Jassonirvana* Baker.1923, *Philipp. J. Sci.* 23 : 399.Type—*Jassonirvana lineata* Baker (Luzon).*Kana* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 285.Type—*Kana thoracica* Distant (Ceylon).*Kosasia* Distant (synonym of *Hodoedoecus* Jacobi).1910, *Ins. Transvaal.* 10 : 240.Type—*Kosasia typica* Distant (Natal).*Macroceratogonia* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 323.Type—*Macroceratogonia aurea* Kirkaldy (Queensland).*Mohunia* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 272.Type—*Mohunia splendens* Distant (Tenasserim).*Mukaria* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 269.Type—*Mukaria penhimoides* Distant (Ceylon).*Narecho* Jacobi.1910, *Sjöstedts Kilimandjaro Meru Exp.* 12 : 127.Type—*Narecho pallioviridis* Jacobi (East Africa).*Neonirvana* Oman.1936, *Pan-Pacific Ent.* 12 : 116.Type—*Neonirvana hyalina* Oman (Costa Rica).*Nirvana* Kirkaldy.1900, *Entomologist* 33 : 293.Type—*Nirvana pseudommatus* Kirkaldy (Ceylon).*Nirvanoides* Baker.1923, *Philipp. J. Sci.* 23 : 396.Type—*Nirvanoides amboinensis* Baker (Amboina).*Occinirvana* Evans.1943, *Trans. Roy. Soc. W. Aust.* 27 : 156.Type—*Occinirvana eborea* Evans (Western Australia).*Omaranus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 5.Type—*Omaranus typicus* Distant (Calcutta).*Oniella* Matsumura.1912, *Annot. Zool. Japon.* 8 : 46.Type—*Oniella leucocephala* Matsumura (Japan).

Ophiuchus Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 23.Type—*Ophiuchus princeps* Distant (India).*Parablotettix* Matsumura (synonym of *Mukaria* Distant).1912, *J. coll. Agric. Sapporo* 4 : 280.Type—*Parablotettix maculatus* Matsumura (Formosa).*Paraciacadula* Osborn.1935, *Bull. Bishop Mus.* 114 : 260.Type—*Paraciacadula coniceps* Osborn (Marquesas Islands).*Pseudobalbillus* Jacobi.1912, *Ergebn. Deutsch. Zentr. Afrik. Exp.* 4 : 37.Type—*Pseudobalbillus protudens* Jacobi (Central Africa).*Pseudonirvana* Baker (synonym of *Sophonias* Walker).1923, *Philipp. J. Sci.* 23 : 386.Type—*Pseudonirvana sandakanensis* Baker (Borneo).*Pythnirvana* Baker.1923, *Philipp. J. Sci.* 23 : 397.Type—*Pythnirvana muiri* Baker (Amboina).*Sophonias* Walker.1869, *J. Linn. Soc. Lond. Zool.* 10 : 327.Type—*Sophonias rustelum* Walker (Mysol).*Stenometopius* Matsumura.1914, *J. coll. Agric. Sapporo* 5 : 217.Type—*Stenometopius formosanus* Matsumura (Formosa).*Stenotortor* Baker.1923, *Philipp. J. Sci.* 23 : 377.Type—*Stenotortor inocarpi* Baker (Singapore).*Tortor* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 42.Type—*Tortor daulias* Kirkaldy (Queensland).*Taxonomic Notes.*

Until 1923, when Baker recognised the family NIRVANIDAE, the several genera listed above had been referred to various sub-families. *Nirvana*, which Kirkaldy originally considered to be close to *Spanbergiella*, was later (1907) referred by him to the TYPHLOCYBINAE, while Melichar (1903) placed this genus in the Acocephalini. The genotype of *Omaranus*, which Distant referred to the TETTIGONIELLINAE, and the genotype of *Didius*, which the same author referred to the JASSINAE, have been shown by Pruthi (1934) to be the female and male respectively of a single species. Haupt (1929) mentions that he has examined the type of *Uzelina* and considers that this genus belongs to the NIRVANIDAE, but I am unable to accept this opinion since Melichar's figure of the genotype is an illustration of an undoubted Penthimiid.

Discussion of the NIRVANINAE.

While this sub-family is undoubtedly a natural, and not an artificial, grouping of genera, its affinities are obscure, though it may possibly be derived from the Aphrodini.

An unusual structural feature is displayed in the heads of two species, *Occinirvana eborea* (fig. 17m, n) and *Omaranus typicus* (fig. 17h, i).

In both these species the elongation of the head has taken place between the eyes and the antennae, and not, as is usual, between the apex of the coronal suture and the apex of the crown (fig. 17f, g). The result of this elongation has been to expose and attenuate the anterior tentorial pits and to leave the antennal ledges lying actually anterior to the antennae.

Macropsides.

The various sub-families in this division of the JASSIDAE consist of diverse elements which represent several distinct lines of descent from an early jassid stem. They may be divided into five groups, of which the first comprises the MACROPSINAE, AGALLIINAE, AUSTRAGALLOIDINAE, MELICHARELLINAE, COELIDIINAE and NEOCOELIDINAE; the second the TYPHLOCYBINAE; the third the TARTESSINAE; and the fourth and fifth groups the JASSINAE and the EUSCELINAE respectively.

The first of these groups contains leaf-hoppers which vary in coloration, but are seldom uniformly dull brown as are so many of the Ulopides. They possess a small frons, which is restricted to the face of the head, and associated with this feature is the fact that the crown is usually small and seldom produced to any considerable extent in front of the eyes.

MACROPSINAE.

As well as those genera which are undoubtedly related to *Macropsis* and *Oncopsis* I am including in this sub-family two genera, *Nionia* and *Magnentius*, which are of uncertain position. Hence the necessity for the division of the MACROPSINAE into two tribes, the Macropsini and the Nioniini.

Macropsini (fig. 18).

Distribution.

All the principal geographical regions, but apparently poorly represented in both the Oriental and the Neotropical regions.

Size, Coloration and General Appearance.

The Macropsini range from 4 to 8 mm. in length and in colour are either green or some shade of brown, or orange, or they are partly grey, or black, and they may have a mottled appearance. In appearance they are wedge-shaped, with the face steeply reflexed and the head and thorax usually punctate.

Food-plants and Habits.

With a few known exceptions all the Macropsini are arboreal and each species is restricted to a single, or to a limited, range of food-plants. In Australia they occur on several broad-leaved, evergreen shrubs, but I have never taken them on eucalypts, which is the principal food of most other groups of arboreal jassids in that continent. Hartzell (1937) has given an account of the bionomics of *Macropsis trimaculata* Fitch

which occurs on *Prunus* in North America; other North American species feed on *Salix* and *Betula* (Knowlton and Allen, 1936), while British representatives have been recorded from these trees and from *Ulmus* and *Alnus* (Edwards, 1896). Edwards records *Macropsis nanus* H. S. from short grass in dry places.

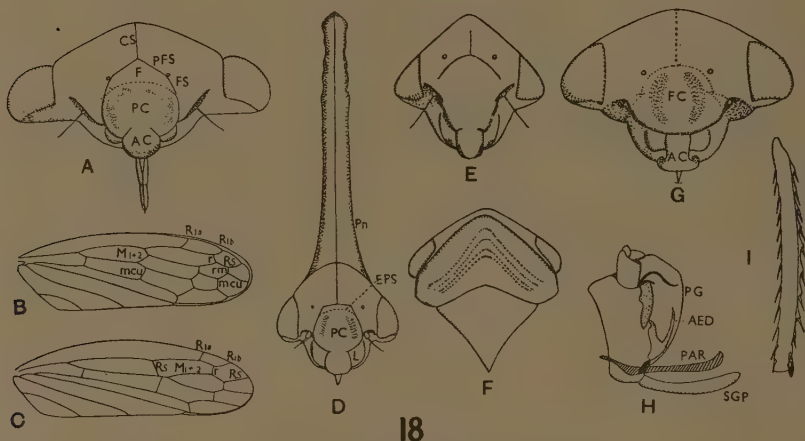


FIG. 18.

A, *Stenoscopus drummondi* Ev., head; B, *Macropsis citrinus* Ev., tegmen; C, *Macropsis virescens* Fabr., tegmen; D, *Stenopsoides turneri* Ev., head and pronotum; E, *Macropsis virescens*, head; F, *M. virescens*, head and thorax, dorsal aspect; G, *Oncopsis pullus* Ev., head; H, *Macropsis filicis* Ev., male genitalia; I, *Oncopsis aeneus* Ev., hind tibia.

Description.

Head. The labium is of moderate length and the ante-clypeus, which is usually somewhat swollen, is often incompletely separated from the post-clypeus. The anterior lateral margins of the post-clypeus are short and are often approximately transverse and in alignment with the antennal ledges; occasionally the outlines of this part of the post-clypeus are obscure. The lora are usually swollen and the maxillary plates narrow. The antennae are short, the antennal ledges prominent and the antennal depressions deep. The post-clypeus, or the fronto-clypeus, which is generally approximately circular in outline, usually has a pair of crescent-shaped markings on its surface (the impressions of the cibarial muscles). The frons, which is always entirely on the face of the head, and which lies at some distance from the posterior margin, is seldom distinct from the post-clypeus, although frontal and post-frontal sutures are frequently retained. The ocelli are always on the face, and a crown, if developed at all, is very narrow.

Thorax. The pronotum is curved anteriorly, narrow laterally, and approximately transverse posteriorly; it is usually declivous and sometimes humped; it may even be considerably produced in front of the head.

Legs. The tibiae are quadrilateral in section and the hind tibiae are armed with short, strong spines.

Tegmina. The venation is often of the normal jassid type, but sometimes there is an additional cross-vein present between M_{3+4} and Cu_{1a} , and there may be as well two cross-

veins between R_s and M_{3+4} . Although these two latter cross-veins formed part of the ancestral venational scheme, their retention in present-day jassids is an unusual feature.

Male-genitalia. Both the sub-genital plates and the parameres are long and narrow, and the ninth sternite has lost its separate identity.

Genera of the Macropsini.

Galboa Distant.

1909, *Trans. Linn. Soc. Lond. (Zool.)* **13** : 45.

Type—*Galboa typica* Distant (Seychelles).

Macropsis Lewis.

1834, *Trans. ent. Soc. Lond.* **1** : 49.

Type—*Cicada virescens* Fabricius (Westwood, 1840) (Germany).

Neopsis Oman.

1936, *Univ. Kansas Sci. Bull.* **24** : 353.

Type—*Pediopsis elegans* Van Duzee (Jamaica).

Oncopsis Burmeister.

1838, *Gen. Ins.* **1** : (no pagination).

Type—*Cicada flavicollis* Linnaeus (Westwood, 1840) (Europe).

Parasitades Pruthi.

1936, *Mem. Ind. Mus.* **11** : 106.

Type—*Parasitades baileyi* Pruthi (Sikkim).

Pediopsis Burmeister (synonym of *Macropsis* Lewis).

1838, *Gen. Ins.* **1** : (no pagination).

Type—*Jassus tiliae* Germar (Germany).

Stenopsoides Evans.

1943, *Trans. Roy. Soc. W. Aust.* **27** : 153.

Type—*Stenopsoides turneri* Evans (Western Australia).

Stenoscopus Evans.

1934, *Trans. Roy. Soc. S. Aust.* **58** : 166.

Type—*Stenoscopus drummondi* Evans (Western Australia).

Taxonomic Notes.

Until 1939b, when I erected a new family, the MACROPSIDAE, the genera listed above had been associated with *Agallia*, *Idiocerus*, and *Jassus* (*Bythoscopus*) in the BYTHOSCOPIINAE. The segregation of these genera has since been accepted by other workers; Medler (1942) and Oman (1943) have referred to the group as the Macropsini and MACROPSINAE respectively, and Ossiannilsson (1946) to it as the MACROPSIDAE.

Nioniini (fig. 19).

Distribution.

Southern India and North and South America.

Size, Coloration and General Appearance.

Species in the two genera contained in the Nioniini are 4 to 5 mm. in length and entirely black or black and reddish-brown in colour. In appearance they are broadly wedge-shaped, and the head and the thorax are either punctuate or rugose.

Food-plants and Habits.

Nionia palmeri Van Duzee occurs on grasses and herbaceous plants in old pastures and waste places (De Long, 1923).

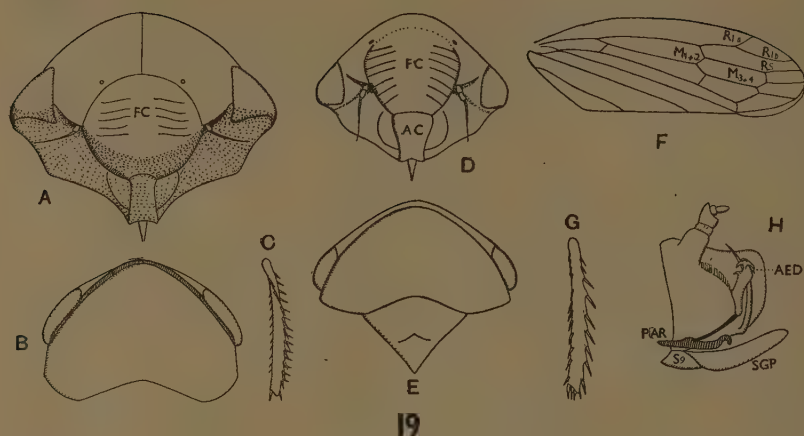


FIG. 19.

A, *Magnentius clavatus* Pruthi, head; B, *M. clavatus*, head and pronotum, dorsal aspect; C, *M. clavatus*, hind tibia; D, *Nionia gagatinus* Breddin, head; E, *N. gagatinus*, head and thorax, dorsal aspect; F, *N. gagatinus*, tegmen; G, *Nionia palmeri* Van Duzee, hind tibia; H, *N. palmeri*, male genitalia.

Description.

Head. The labium is of moderate length; the ante-clypeus is separated from the post-clypeus by a well-defined, transverse suture; the lora are flat and the maxillary plates wide. No trace remains of a separate frons, and the fronto-clypeus, which is circular in outline and bears transverse muscle impressions, is confined entirely to the face of the head. Both frontal and post-frontal sutures are retained; the antennal ledges are prominent and the antennal depressions deep. The ocelli are on the face, close to the curve of the frontal and postfrontal sutures, and the crown is narrow.

Thorax. The pronotum, which is heart-shaped, is slightly declivous.

Legs. The fore and middle tibiae are rounded, and the hind tibiae, which are flattened, have an armature of short, strong spines.

Tegmina. In *Nionia* the venation is complete; the veins of *Magnentius clavatus* are raised in relief and there may be one or a few additional cross-veins.

Genera comprised in the *Nioniini*.

Magnentius Pruthi.

1930, *Mem. Ind. Mus.* 11: 6.

Type—*Magnentius clavatus* Pruthi (South India).

Nionia Ball.

1915, *Proc. biol. Soc. Wash.* 28: 165.

Type—*Goniagnathus palmeri* Van Duzee (South America).

Taxonomic Notes.

Opinions differ as to the true position of *Nionia*. Ball (1915) considered that it resembled both *Tartessus* and *Pediopsis*; Osborn (1920) that it resembled *Tartessus*, while Lawson (1920) referred it to the Acucephalini. Oman (1936) at one time supported the opinion that *Nionia* was related to *Tartessus*, though considered it closer to *Thymbris*;

later (1943) he erected a new sub-family, the NIONIINAE, for this single genus. *Magnentius* was referred by Pruthi to the BYTHOSCOPIINAE.

Discussion of the MACROPSINAE.

Nionia has been associated with *Magnentius* in a separate tribe of the MACROPSINAE because species in these two genera resemble each other both in coloration and in shape, and have also several structural features in common. Their distribution is unusual, but the only two genera of the AETALIONIDAE are likewise restricted to South America and Southern India.

Certain primitive features of the Macropsini have already been discussed (p. 110), and I have suggested that insects in this tribe lie close to the base of one of the lines of jassid descent. Their pre-jassid ancestors were probably related to membracids belonging to the sub-family CENTROTINAE, since species in the genera *Melizoderes* Blanchard and *Orekthen* Funkhouser, both of which belong to the CENTROTINAE, and are confined to Chile, strikingly resemble Macropsids. Not only do they resemble them in head-structure, but they also have the pronotum enlarged in a similar way to that in such jassid species as *Oncopsis tepperi* Evans. Furthermore the armature of their hind tibiae, though typically membracid in character, is not far removed from that of the Macropsini. The venation of the tegmen of *Melizoderes cuneata* Butler is of the jassid, rather than the membracid type, since Cu_1 is distinct for its whole length and M is fused basally with R. However, the venation of the tegmen of the Macropsini is more complete than that of *M. cuneata* since in the latter M_{1+2} is absent. It is of interest to note that both of the two genera of the Macropsini which have retained the greatest number of primitive characteristics (*Stenoscopus* and *Stenopsoides*) are confined to Western Australia.

AGALLIINAE (fig. 20).

Distribution.

All the principal geographical regions, with the possible exception of Australia. (The single species, *Nehela torrida* Evans, which has been described from Australia, is almost certainly a recent introduction.)

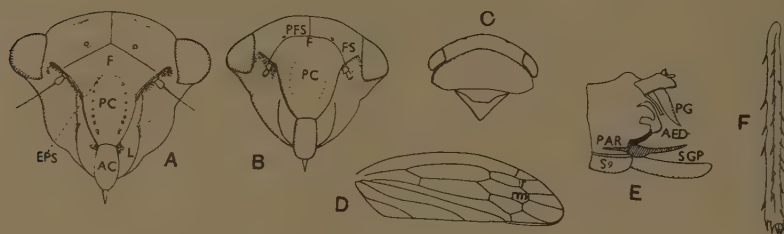
Size, Coloration and General Appearance.

The AGALLIINAE comprise small, narrowly wedge-shaped leaf-hoppers, which range from 2 to 9 mm. in length. The majority are some shade of brown in colour and have characteristic dark brown markings on the crown and pronotum; others are black or grey, or so pale as to be almost colourless, while a few are black and scarlet. A small number are punctate and forms occur in which the tegmina are reduced to a varying extent.

Food-plants and Habits.

A few records exist of species living on trees, thus *Agalliopsis cervina* Oman (1935) has been taken on *Quercus*. The greater number, however, is confined to herbaceous plants and has been recorded from lucerne,

potatoes, carrots, sugar-cane, *Artemesia*, *Atriplex* and *Alopappus* (Knowlton and Allen, 1936; Osborn, 1929). Edwards (1896) records *Agallia venosa* Fall. as occurring at the roots of grass in England.



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FIG. 20.

A, *Euragallia furculata* Osb., head; B, *Agallia puncticeps* Germ., head; C, *A. puncticeps*, head and thorax, dorsal aspect; D, *A. puncticeps*, tegmen; E, *Agallia venosa* Fall., male genitalia; F, *Euragallia furculata*, hind tibia.

Description.

Head. The head is approximately triangular in shape. The labium is of medium length, the ante-clypeus projects beyond the maxillary plates, the maxillary plates are of moderate width and a vestigial maxillary suture may be retained. The post-clypeus, on which the impressions of the cibarial muscles are often visible as round spots arranged in an oval pattern, is sometimes separated from the frons by a vestigial epistomal suture, and the frons is always entirely facial in position. The frontal and postfrontal sutures often form a wide inverted V and the outer edge of each lorum is sometimes joined to the corresponding anterior tentorial pit by a distinct fold or ridge. The antennal depressions are deep, and the antennal ledges, which are prominent and oblique, are approximately in alignment with the sides of the post-clypeus. The ocelli are always situated on the face, although in forms with an inflated post-clypeus they may be also visible in dorsal aspect: their position is not constant and though they are sometimes close to the junction of the frontal and post-frontal sutures, they may also lie at some distance from these sutures, or be close together on either side of the coronal suture. The crown, which is of even width with the eyes, forms a continuous curved surface with the face of the head.

Thorax. The pronotum, which is small, is narrow laterally and the scutellum has frequently a transverse median depression.

Legs. The fore and middle tibiae are rounded, and the hind tibiae, which are quadrilateral in section, have a sparse armature of weak spines.

Tegmina. The venation if the tegmen is complete and the appendix is narrow. Forms occur in which the tegmina are reduced in size to a varying extent.

Genera comprised in the AGALLIINAE.

Aceratagallia Kirkaldy.

1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3: 30.

Type—*Bythoscopus sanguinolentus* Provancher (North America).

Agallia Curtis.1833, *Ent. Mag.* 1 : 193 (Jan.).Type—*Agallia consobrinus* Curtis (England).*Agalliana* Oman.1933, *Tech. Bull. U.S. Dept. Agric.* 372 : 70.Type—*Bythoscopus sticticollis* Stål (Central America).*Agalliopsis* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 31.Type—*Jassus novellus* Say (North and South America).*Agalliota* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 351.1938, *Ann. Carnegie Mus.* 25 : 393.Type—*Agallia punctata* Oman (Tropics and Subtropics of Western Hemisphere.)*Austroagallia* Evans (synonym of *Nehela* B.W.).1936, *Pap. Roy. Soc. Tasm.* 1935 : 70.Type—*Austroagallia torrida* Evans (Australia).*Bergallia* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 350.Type—*Bythoscopus signatus* Stål (South America).*Brasa* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 352.Type—*Macropsis rugicollis* Dozier (Haiti).*Ceratagallia* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 4 : 61.1939, *J. Wash. Acad. Sci.* 29 : 529.Type—*Agallia bigeloviae* Baker (semi-arid parts of North America).*Durgades* Distant.1912, *Ann. Mag. nat. Hist.* (8) 10 : 608.Type—*Durgades nigropictus* Distant (Northern India).*Euragallia* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 351.Type—*Agallia furculata* Osborn (South America).*Gunhilda* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 88.Type—*Gunhilda noctua* Distant (South India).*Igerna* Kirkaldy (new name for *Pachynus* Stål, a synonym of *Nehela* B.W.).1903, *Wien. ent. Zeit.* 22 : 13.*Ionia* Ball.1933, *Bull. Brooklyn ent. Soc.* 28 : 225.Type—*Ionia triunata* Ball (North America).*Nehela* Buchanan White.1878, *Proc. zool. Soc. Lond.* 1878 : 473.Type—*Nehela vulturina* Buchanan White (St. Helena).*Pachynus* Stål (preoccupied, see *Igerna* Kirkaldy).1866, *Hemipt. Africana* 4 : 127.Type—*Bythoscopus (Oncopsis) bimaculicollis* Stål (South Africa).*Stonasl* Buchanan White.1878, *Proc. zool. Soc. Lond.* 1878 : 472.Type—*Stonasl undulata* Buchanan White (St. Helena).*Taxonomic Notes.*

The sub-family AGALLIINAE, as recognised by Kirkaldy (1906), was synonymous with the BYTHOSCOPIINAE of several authors, and comprised

a heterogeneous collection of unrelated genera. The first to appreciate the distinctive characteristics of this group was Haupt (1929), who referred *Agallia* to a tribe, the Agalliini, in which he also included several other genera, which in my opinion belong elsewhere. Recently the group has been recognised as a family (Evans, 1939b) and as a sub-family (Oman, 1943).

Discussion of the AGALLIINAE.

The AGALLIINAE, which, like the MACROPSINAE, are close to the base of the jassid stem, comprise a remarkably homogeneous group of genera which flourish especially in South America. Certain primitive features associated with the structure of the head are the retention, in certain forms, of an epistomal suture and maxillary sutures, and the association of the lora with the tentorial pits.

AUSTROAGALLOIDINAE (fig. 21).

Distribution.

Australia.

Size, Coloration and General Appearance.

The AUSTROAGALLOIDINAE range in length from 5 to 8 mm., and in colour they are either pink, pale yellowish-green, grey, brown, orange or yellow. They are narrowly wedge-shaped and the tegmina, which are usually hyaline, are steeply tectiform. The head and thorax are rugose and sexual dimorphism occurs.

Food-plants and Habits.

All species, so far as is known, feed on eucalypts.

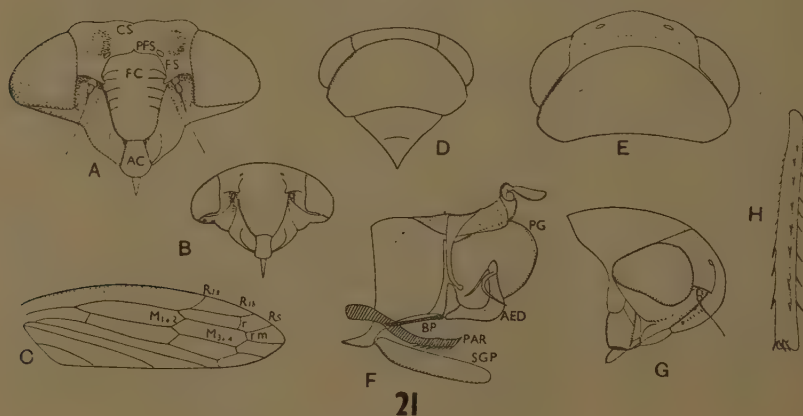


FIG. 21.

A, *Austroagalloides agalliae* Ev., head; B, *Austroagalloides brunnea* Ev., head; C, *A. brunnea*, tegmen; D, *A. brunnea*, head and thorax, dorsal aspect; E, *Austroagalloides rosea* Ev., head and pronotum, dorsal aspect; F, *A. rosea*, male genitalia; G, *A. rosea*, hind tibia.

Description.

Head. The head, the width of which exceeds the length, is flexed in three distinct planes, consisting of the crown, the face as far as the antennal ledges, and the face anterior to the antennal ledges. The labium is short and the ante-clypeus projects beyond the maxillary plates. The post-clypeus and the frons are fused and form a single sclerite, and frontal sutures are always, and postfrontal sutures sometimes, retained. The antennal ledges, which are prominent and transverse, lie midway along the anterior margins of the eyes and they may slightly overlap on to the fronto-clypeus; the antennal depressions are narrowly trough-shaped. The ocelli, which are situated on the face, close to the posterior apices of the frontal sutures, may be visible also in dorsal aspect, and the eyes, which are large, are sometimes prominent.

Thorax. The pronotum, which is narrow laterally, has the anterior margin curved and the posterior margin approximately transverse.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are quadri-lateral in section, have an armature of small, weak spines.

Tegmina. The tegmen, which has complete venation and a narrow appendix, has rows of raised dots, either on, or alongside, the veins.

Male Genitalia. The pygophore is separated from the ninth segment by a suture, and the ninth sternite, though not a distinct sclerite, is separated from the rest of the segment by a narrow isthmus. The aedeagus is linked with the anal segment by an apodeme, and the basal plate is long.

Genera comprised in the AUSTROAGALLOIDINAE.

Austroagalloides Evans.

1936, *Pap. Roy. Soc. Tasm.* 1935: 70.

Type—*Austroagalloides karoondae* Evans (South Australia).

Taxonomic Notes.

The sole genus in this sub-family was originally referred to the BYTHOSCOPIIDAE; later I created a separate family for its reception (1939b).

Discussion of the AUSTROAGALLOIDINAE.

I have previously suggested (1939b) that this group of leaf-hoppers may form part of the autochthonous xerophytic fauna which developed in Australia during late Tertiary times. In certain features its representatives resemble the MELICHARELLINAE and it is possible that the two groups have a common origin, their present distinctive features having developed as a result of long geographical isolation.

MELICHARELLINAE (fig. 22).*Distribution*

Tunisia, Algeria, Turkestan, Persia and Northern India (Eremian sub-region).

Size, Coloration and General Appearance.

The MELICHARELLINAE range in length from 5 to 9 mm. and in colour are either pale green, grey, or brown. They are, in shape, either long and narrow and of delicate appearance, or they are robust and wedge-shaped.

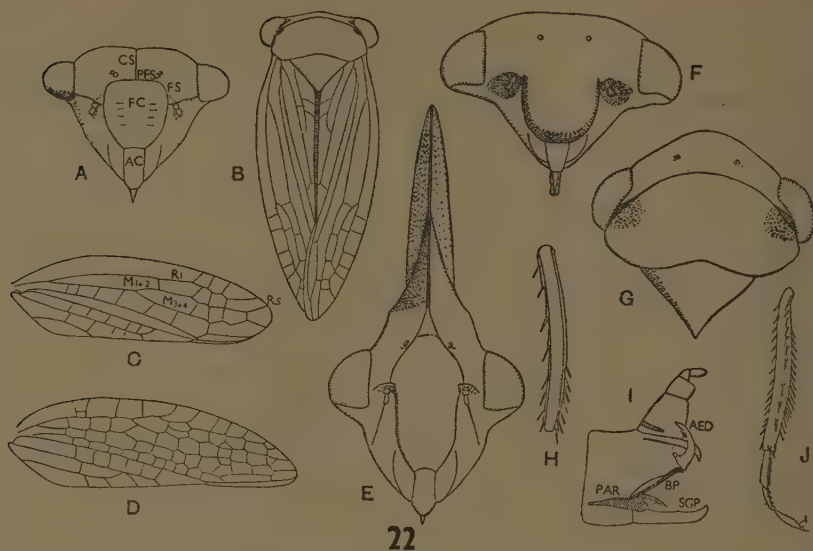


FIG. 22.

A, *Melicharella planifrons* Melichar, head; B, *M. planifrons*; C, *Symphypygia leopardina* Haupt, tegmen; D, *Adelungia calligoni* Oshanin, tegmen; E, *A. calligoni*, head; F, *Bergevinia ahnegeri* Mel., head; G, *B. ahnegeri*, head and thorax, dorsal aspect; H, *Melicharella decora* Lindb., hind tibia; I, *Symphypygia leopardina*, male genitalia; J, *S. leopardina*, hind tibia and tarsus.

Food-plants and Habits.

Achrus nigronevrosus Lindberg has been recorded from Tamarisk (Lindberg, 1924) and *Melicharella hieroglyphica* Bergevin has been taken on *Calligonum comosum* in Tunis (de Bergevin, 1925).

Description.

Head. The labium is short, and the ante-clypeus, which often has apical bristles, projects beyond the maxillary plates. The post-clypeus, which may be either flat or swollen, is continuous with the frons and the latter, which is confined to the face, is sometimes limited posteriorly by frontal and postfrontal sutures. The antennal ledges, which lie close to the anterior corners of the eyes, are prominent and transverse, and the antennal depressions are of moderate depth. The ocelli are on the face, close to the frons, but in those forms in which the fronto-clypeus is swollen they may be visible also from above. The crown, except in *Adelungia*, is narrow and the eyes may be prominent.

Thorax. The pronotum is narrow laterally and may be declivous, and the anterior margin is approximately parallel to the hind margin.

Legs. The tibiae may be either rounded or flattened and the spines on the hind tibiae are usually weak.

Tegmina. The tegmina are long and narrow and the venation is reticulate.

Genera comprised in the MELICHARELLINAE.

Achrus Lindberg.

1924, *Notulae Ent.* 4 : 108.

Type—*Achrus nigronevrosus* Lindberg (Transcaspia).

Adelungia Melichar.

1902, *Ann. Mus. zool. St. Petersburg.* 7 : 134.

Type—*Adelungia elegans* Melichar (Persia).

Ahngeria Melichar (preoccupied, see *Melicharella* Semenov).

1902, *Wien. ent. Zeit.* 21 : 76.

Type—*Ahngeria planifrons* Melichar (Transcaspia).

Bergevina (nom. nov. pro *Macroceps* Melichar, 1902 nec. Sign. 1879.)

Type—*Macroceps ahngeri* Melichar (Transcaspia).

Melicharella Semenov (new name for *Ahngeria* Melichar).

1902, *Rev. russe Ent.* 2 : 190, 353.

Paramacroceps Bergevin.

1926, *Bull. Soc. Hist. nat. Afr. Nord.* 16 : 30.

Type—*Paramacroceps fouquei* Bergevin (Algeria).

Peyerimhoffiella Bergevin.

1928, *Bull. Soc. Hist. nat. Afr. Nord.* 19 : 276.

Type—*Peyerimhoffiella galeata* Bergevin.

Platyproctus Lindberg.

1924, *Notulae Ent.* 4 : 112.

Type—*Platyproctus tessellatus* Lindberg (Transcaspia).

Symphypyga Haupt.

1917, *Wien. ent. Zeit.* 36 : 239.

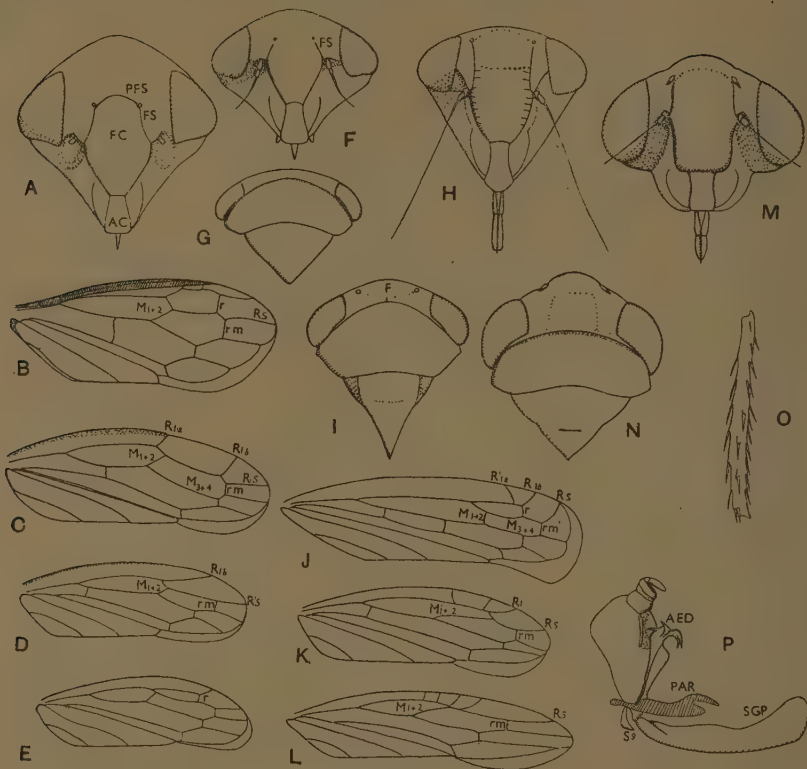
Type—*Symphypyga obsoleta* Haupt (Buchara).

Taxonomic Notes.

All the above genera were at one time referred to the BYTHOSCOPIIDAE (Lindberg, 1924 ; Pruthi, 1930), apart from *Adelungia* which was placed in the LEDRIDAE by Haupt (1929) and in the JASSINAE, Koebeliaria, by Oshanin (1912). De Bergevin, who in 1925 had suggested that *Melicharella* formed a link between *Bythoscopus* and *Acocephalus*, in 1926 proposed the sub-family name, MACROCEPSINAE, for the group ; later (1927) he altered the name to the MELICHARELLINAE, because *Macroceps*, which is an Australian genus, is not, as was formerly thought, closely related to any of the genera comprised in the MELICHARELLINAE.

Discussion of the MELICHARELLINAE.

The most striking leaf-hoppers in this sub-family are contained in the genera *Adelungia* and *Peyerimhoffiella* ; both have a keeled, declivous pronotum and the heads of *Adelungia* spp. are anteriorly produced. While the character of a produced head is of no especial significance it is of interest, because it is an unusual development for a jassid with a ventral frons. I can find no record of *Adelungia* having been previously referred to the MELICHARELLINAE, but I have no hesitation in referring it to this sub-family, because of the reticulate venation of its tegmina, its basic cephalic characters, and its geographical distribution.



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FIG. 23.

A, *Chunra gigantea* Dist., head; B, *C. gigantea*, tegmen; C, *Chunroides wallabensis* Ev., tegmen; D, *Rotifunkia guttifera* Walk., tegmen; E, *Idiocerus vitreus* Fabr., tegmen; F, *I. vitreus*, head; G, *I. vitreus*, head and thorax, dorsal aspect; H, *Idiotettix fasciatus* Osb., head; I, *I. fasciatus*, head and thorax, dorsal aspect; J, *I. fasciatus*, tegmen; K, *Tumocerus grandis* Ev., tegmen; L, *Gnatia angustata* Ev., tegmen; M, *Tumocerus varius* Ev., head; N, *T. varius*, head and thorax, dorsal aspect; O, *Idiocerus candidus* Ev., hind tibia; P, *I. seckeri* Ev., male genitalia.

IDIOCERINAE (fig. 23).

Distribution.

All the principal geographical regions.

Size, Coloration and General Appearance.

The IDIOCERINAE range in length from 3 to 9 mm. and in colour are either brown, bronze, orange, yellow, green or black. In appearance they are either broadly, or narrowly, wedge-shaped and their tegmina, which are usually hyaline, have an extensive apical overlap.

Food-plants and Habits.

In the Oriental region certain species are injurious to mangoes (*Mangifera indica*) (Serrano and Palo, 1933); in Europe and North America *Salix* and *Populus* are favoured food-plants; while in Australia several species feed on eucalypts.

Description.

Head. The labium is of medium length and the ante-clypeus projects beyond the narrow maxillary plates. The post-clypeus is almost invariably continuous with the frons, and the latter, which is always on the face of the head, is bounded laterally by frontal sutures, and sometimes also posteriorly by postfrontal sutures. The antennal ledges, if present, are generally situated close to the anterior angles of the eyes and the antennal depressions are of moderate depth; the antennae are of variable length, and in some species those of the males have disc-like terminal swellings. The ocelli, which are always on the face of the head, but may also be visible from above, lie close to the posterior apices of the frontal sutures, and the crown, which is usually of even width with the eyes, forms a continuous curved surface with the face.

Thorax. The pronotum, which is short, is narrow laterally and the anterior and posterior margins are usually parallel with each other.

Legs. The fore and middle tibiae are rounded, and the hind tibiae, which are somewhat flattened, usually have an armature of weak spines but sometimes they have two rows of strong spines.

Tegmina. The tegmina, which may be long and broad, or short and narrow, have a wide appendix, and the costal border is sometimes broadly thickened. The venation, which is extremely variable, may be complete or reduced. The most usual reduction is the loss of R_{1a} , but M_{1+2} is also sometimes missing and R_3 may be fused with M_{3+4} . In addition, the complete complement (three) of cross-veins lying between M and Cu_1 is seldom developed and cross-vein r is sometimes absent.

Male Genitalia. The male genitalia, which have a characteristic appearance, are narrower ventrally than dorsally, and the sub-genital plates are long and apically wide.

*Genera comprised in the IDIOCERINAE.**Austrocerus* Evans.

1941, *Trans. Roy. Soc. S. Aust.* 65 : 37.

Type—*Austrocerus emarginatus* Evans (Kangaroo Is., South Australia).

Balocha Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 189.

Type—*Balocha tricolor* Distant (Tenasserim).

Busonia Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 198.

Type—*Busonia amentata* Distant (Assam).

Chunra Distant.

1907, *Faun. Brit. Ind. Rhyn.* 4 : 193.

Type—*Jassus puncticosta* Walker (Malaya).

Chunroides Evans.

1947, *Trans. R. ent. Soc. Lond.* 98 : 254.

Type—*Chunroides wallabensis* Evans (British Guiana).

Exolidia Osborn.

1923, *Ann. Carnegie Mus.* 15 : 75.

Type—*Exolidia picta* Osborn (Brazil).

Gnatia Evans.

1943, *Trans. Roy. Soc. W. Aust.* 27 : 150.

Type—*Gnatia angustata* Evans (Western Australia).

Idiocerella Evans.1941, *Trans. Roy. Soc. S. Aust.* 65 : 39.Type—*Idiocerella obscura* Evans (Kangaroo Is., South Australia).*Idiocerinus* Baker.1915, *Philipp. J. Sci.* 10 : 341.Type—*Idiocerinus melichari* Baker (Luzon).*Idioceroides* Matsumura.1912, *J. Coll. Agric. Sapporo* 4 : 324.Type—*Idioceroides tettigoniiformis* Matsumura (Formosa).*Idiocerus* Lewis.1836, *Trans. ent. Soc. Lond.* 1 : 47.Type—*Idiocerus stigmaticollis* Lewis (= *adustus* H.S.) (Britain).*Idioscopus* Baker.1915, *Philipp. J. Sci.* 10 : 338.Type—*Idiocerus clypealis* Lethierry (India).*Idiotettix* Osborn.1929, *Ann. ent. Soc. Amer.* 22 : 465.Type—*Thamnotettix magnificus* Osborn (Bolivia).*Ipocerus* Baker.1915, *Philipp. J. Sci.* 10 : 323.Type—*Ipocerus kirkaldyi* Baker (Palawan).*Iposcopus* Baker.1915, *Philipp. J. Sci.* 10 : 320.Type—*Iposcopus distant* Baker (Mindanao).*Macrocerus* Evans.1941, *Trans. Roy. Soc. S. Aust.* 65 : 39.Type—*Macrocerus minutus* Evans (Kangaroo Is., South Australia).*Megipocerus* Zakhvatkin.1945, *Proc. R. ent. Soc. Lond.* (B) 14 : 3.Type—*Megipocerus mordvilkoii* Zakhvatkin (Eastern Siberia).*Pedioscopus* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 349.Type—*Pedioscopus philenor* Kirkaldy (Queensland).*Rotifunkia* China.1926, *Ann. Mag. nat. Hist.* (9) 17 : 672.Type—*Paropia guttifera* Walker (West Africa).*Tumocerus* Evans.1943, *Trans. Roy. Soc. W. Aust.* 27 : 149.Type—*Tumocerus varius* Evans (Western Australia).*Zinneca* Amyot and Serville (synonym of *Idiocerus* Lewis).1843, *Hist. Nat. des. Ins. Hemipt.* : 579.Type—*Zinneca flavidorsum* Amyot and Serville (Eastern North America).*Taxonomic Notes.*

Idiocerus and related genera have usually been included in the BYTHOSCOPIINAE or BYTHOSCOPIDAE of various authors (e.g., De Long and Caldwell, 1937). Baker (1915) was the first to appreciate the distinctive characters of this genus and created a tribe, the Idiocerini, in which he also included *Ipo* Kirkaldy (a eurymelid). Oman (1943) likewise holds the opinion that *Idiocerus* and *Eurymela* are related and has referred the former to the EURYMELINAE. Haupt (1929) associated *Idiocerus* with *Agallia* in a tribe, the Agallini (BYTHOSCOPIINAE), and in 1939b I raised the group to family rank.

Discussion of the IDIOCERINAE.

The IDIOCERINAE comprise a group of distinctive and, on the whole, easily recognisable genera. Such resemblance as they may have to representatives of the EURYMELINAE is entirely of a superficial nature. Two of the genera listed above, *Idiotettix* and *Exolidia*, both of which occur in South America, are only provisionally included in this sub-family; it is possible that further study will show that they represent a distinct tribe or even sub-family. The most generalised genus is *Chunra*, which occurs in the Oriental region, but has close relatives both in Siberia and in British Guiana.

COELIDIINAE¹² (fig. 24).*Distribution.*

The COELIDIINAE occur in all the principal geographical regions. They are especially well represented in the Oriental and Neotropical regions, and in Australia they form part of the Indo-Malayan fauna of North Queensland. In Europe they are represented only by two aberrant genera.

Size, Coloration and General Appearance.

The COELIDIINAE range from 5 to 9 mm. in length and in colour they are usually some shade of brown or black, and they may have an incon-

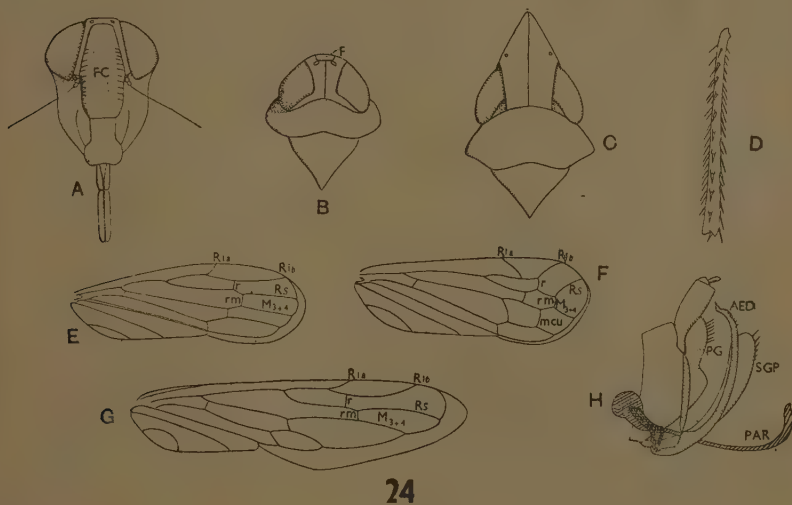


FIG. 24.

A, *Coelidia indicus* Walk., head; B, *C. indicus*, head and thorax, dorsal aspect; C, *Sabimoides cardamomi* Ev., head and thorax, dorsal aspect; D, *S. cardamomi*, hind tibia; E, *Coelidia indicus*, tegmen; F, *Soortana simulata* Dist., tegmen; G, *Doda laudata* Dist., tegmen; H, *Coelidia olitorius* Say, male genitalia.

¹² Formerly known as the JASSINAE. A full explanation of the reasons for this nomenclatorial change has been given by China and Fennah, 1946.

spicuous pattern development. In shape they are long, narrow anteriorly, and broad apically, and sometimes they are brachypterous.

Food-plants and Habits.

Coelidia olitoria Say, a North American species, feeds on shrubs, and has been taken on *Baptisia* (Frost, 1945).

Description.

Head. The head is longer than wide, the labium is long, and the ante-clypeus is broader anteriorly than posteriorly. The narrow post-clypeus, which is parallel-sided, is occasionally separated from the frons by a vestigial epistomal suture. Both frontal and postfrontal sutures are usually retained and the latter generally coincide with the posterior margin of the face. The antennae are long, the antennal depressions shallow, and the antennal ledges, which are short and transverse, are usually close to the anterior corners of the eyes. The ocelli are situated on the margin of the head, between the face and the crown, but in forms with produced heads they lie actually on the crown. The eyes, which are large and depressed below the vertex, overlap the pronotum laterally.

Thorax. The pronotum, which is wide laterally, is considerably broader posteriorly than anteriorly.

Legs. The fore and middle tibiae may be either rounded, or flattened, and the hind tibiae, which are long and somewhat flattened, have a dense armature of spines.

Tegmen. The tegmen, which is usually broadest towards the apex, has a wide appendix. Although species in a few genera have complete venation (*Cyrta*, *Placidus*), they are exceptional, and the venational pattern which is characteristic of the group is illustrated in Fig. 24e, where both M_{1+2} and cross-vein $m-cu_3$ are lacking. An unusual feature of common occurrence in this sub-family is the separation of Cu_2 from the claval suture ; a few forms have reticulate venation.

Genera comprised in the COELIDIINAE.

Aeternus Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 50.

Type—*Aeternus hieroglyphicus* Distant (Tenasserim).

Coelidia Germar.

1821, *Mag. Ent.* 4 : 75.

Type—*Coelidia venosa* Germar (Brazil).

Cyrta Melichar.

1902, *Ann. Mus. zool. St. Petersb.* 1902 : 136.

Type—*Cyrta hirsuta* Melichar (West China).

Daridna Walker (synonym of *Coelidia* Germar).

1858, *List Homopt. Brit. Mus., Suppl.* : 319.

Type—*Daridna subtangens* Walker (Brazil).

Deridna Van Duzee (invalid emendation of *Daridna* Walker).

1917, *Check List Hemipt. Amer.* : 75.

Dharma Distant.

1908, *Faun. Brit. Ind. Rhyn.* 4 : 323.

Type—*Dharma projecta* Distant (Tenasserim).

Doda Distant.

1908, *Rec. Ind. Mus.* 2 : 144.

Type—*Doda laudata* Distant (Siam).

Equeefa Distant (synonym of *Palicus* Stål).

1910, *Ins. Transvaal.* 10 : 243.

Type—*Equeefa castlenawi* Distant (South Africa).

Gabrita Distant.1858, *List Homopt. Brit. Mus., Suppl.* : 254.Type—*Gabrita annulivena* Walker (Tapajos).*Guliga* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 326.Type—*Guliga erebus* Distant (Assam).*Iberia* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 40.Type—*Stegelytra bolivari* Signoret (Spain).*Jassoidula* Osborn.1934, *Ins. Samoa.* 2 : 182.Type—*Jassoidula straminea* Osborn (Samoa).*Jassus* auctt. nec Fabricius (see *Coelidia* Germar).*Kunasia* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 339.Type—*Kunasia nervosa* Distant (Tenasserim).*Limentinus* Distant.1917, *Trans. Linn. Soc. Lond. (Zool.)* 17 : 316.Type—*Limentinus aldabranus* Distant (Seychelles).*Muirella* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 79.Type—*Muirella oxyomma* Kirkaldy (Fiji).*Mukwana* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 317.Type—*Mukwana introducta* Distant (Ceylon).*Nisitra* Walker.1869, *J. Linn. Soc. Lond. (Zool.)* 10 : 327.Type—*Nisitra telifera* Walker (Mysol).*Orthojassus* Jacobi (synonym of *Nisitra* Walker).1914, *Sitz. Ber. Ges. Naturf. Fr. Berlin* 1914 : 382.Type—*Orthojassus philagroides* Jacobi (Formosa).*Palicus* Stål.1866, *Hemipt. Africana* 4 : 120.Type—*Coelidia lineoligera* Stål (South Africa).*Petalopoda* Spanberg (synonym of *Gabrita* Walker).1879, *Öfvers. Vetens-Akad. Förh. Stockh.* 36 : 18.Type—*Petalopoda annulipes* Spanberg (Cayenne).*Placidus* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 341.Type—*Placidus hornei* Distant (North India).*Sabima* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 284.Type—*Sabima prima* Distant (Assam).*Sabimamorpha* Schumacher.1915, *Suppl. Entomol.* 4 : 123.Type—*Sabimamorpha speciosissima* Schumacher (Formosa).*Sabimoides* Evans.1947, *Trans. R. ent. Soc. Lond.* 93 : 254.Type—*Sabimoides cardanomi* Evans (Malaya).*Soortana* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 319.Type—*Soortana simulata* Distant (Ceylon).

Stegelytra Mulsant and Rey.1855, *Ann. Soc. linn. Lyon*. 1855 : 224.Type—*Stegelytra alticeps* Mulsant and Rey (Southern France).*Terulia* Stål.1862, *Köngl. Svensk. Vet.-Akad. Handl.* 3 : 50.Type—*Terulia ferruginea* Stål (Brazil).*Thagria* Melichar.1903, *Homopt. Faun. Ceylon* : 176.Type—*Thagria fasciata* Melichar (Ceylon).*Tharra* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 324.Type—*Tharra labena* Kirkaldy (Queensland).*Tinobregmus* Van Duzee.1894, *Bull. Buff. Soc. Nat. Sci.* 5 : 213.Type—*Tinobregmus vittatus* Van Duzee (Southern U.S.A.).*Toba* Schmidt.1911, *Stettin. ent. Zeit.* 72 : 301.Type—*Toba fasciculata* Schmidt (Sumatra).*Taxonomic Notes.*

For a long period *Coelidia* (*Jassus*) was associated with *Euscelis* and related genera in a sub-family, the JASSINAE, and this sub-family has sometimes been recognised as including also the *Acucephalini* (Lawson, 1920 ; Naudé, 1926). Distant (1908) divided the JASSINAE into numerous tribes, and to two of these, the Thagriaria and the Jassusaria, he referred several of the genera listed above, and as well many unrelated genera. Both Haupt (1929) and Oman (1943) have recognised a sub-family, the JASSINAE, which has the same limits as the one defined above.

Discussion of the COELIDIINAE.

It is difficult to understand why *Coelidia* and related genera, all of which comprise species with most distinctive characteristics, were associated for so long with genera such as *Euscelis*. The most generalised genera of the COELIDIINAE are *Cyrta* and *Placidus*, since species in these genera, as well as retaining a vestigial epistomal suture, have also complete tegminal venation.

NEOCOELIDIINAE (fig. 25).

Distribution.

Nearctic and Neotropical regions.

Size, Coloration and General Appearance.

The NEOCOELIDIINAE range in length from 5 to 8 mm. and in colour are usually orange or yellow. Their most noticeable features are very long antennae and steeply tectiform tegmina.

Food-plants and Habits.

Paracoelidia tuberculata Baker occurs on pines (Baker, 1898) and *Neocoelidia tumidifrons* Gillette and Baker has been taken in "upland pasture" (Osborn, 1897).

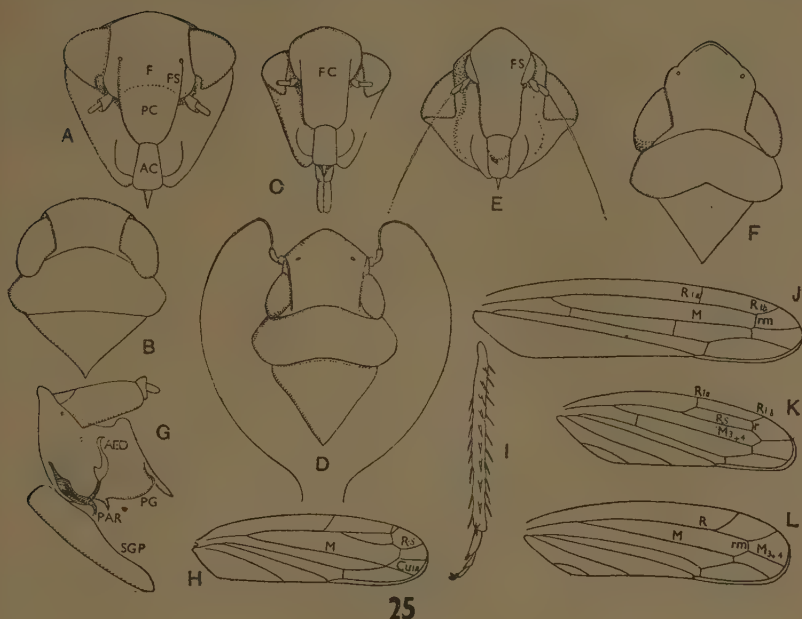


FIG. 25.

A, *Chinaia citrina* Ev., head; B, *C. citrina*, head and thorax, dorsal aspect; C, *Neocoelidia fuscodorsata* Fowler, head; D, *N. fuscodorsata*, head and thorax, dorsal aspect; E, *Paracoelidia tuberculata* Baker, head; F, *P. tuberculata*, head and thorax, dorsal aspect; G, *Neocoelidia distincta* Oman, male genitalia; H, *Neocoelidia fuscodorsata*, tegmen; I, *Neocoelidia distincta*, hind tibia; J, *Chinaia citrina*, tegmen; K, *Neocoelidia distincta*, tegmen; L, *Paracoelidia tuberculata*, tegmen.

Description.

Head. The labium is either short, or of moderate length, and the maxillary plates, or the lora, usually project beyond the ante-clypeus. The post-clypeus is occasionally separated from the frons by a vestigial epistomal suture, but more often the two sclerites are continuous and the frons is entirely ventral in position; while frontal sutures are invariably present, postfrontal ones are only retained in those forms in which the frons extends as far as the hind margin of the face. The antennae are very long and the two basal segments unusually large; the antennal ledges, which are prominent, curved and oblique, sometimes reach as far as the eyes, but more usually they lie alongside the whole length of the frontal sutures. The ocelli may either be on the face of the head, or marginal in position and visible from above, and the eyes are depressed below the level of the vertex. The coronal suture, which may be present or absent, is sometimes replaced by a carina.

Thorax. The pronotum, which is wide laterally, is broader posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded and the hind tibiae, which are somewhat flattened, are armed with strong, evenly spaced spines.

Tegmina. The tegmina are long and narrow, and have a narrow appendix, which continues as far as the apex. The venation, which is often obscure, is reduced to a varying degree and both R_5 and M_{1+2} may be lacking.

Male Genitalia. The sub-genital plates are fused together proximally.

*Genera comprised in the NEOCOELIDIINAE.**Biza* Walker.1858, *List Homopt. Brit. Mus. Suppl.* : 253.Type—*Biza crocea* Walker (Tapajos).*Chinaia* Bruner and Metcalf.1934, *Bull. Brooklyn ent. Soc.* 29 : 120.Type—*Chinaia bella* Bruner and Metcalf (Costa Rica).*Coelidiana* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 397.Type—*Neocoelidia rubrolineata* Baker (Brazil).*Neocoelidia* Gillette and Baker.1895, *Bull. Colorado Exp. Sta.* 31 : 103.Type—*Neocoelidia tumidifrons* Gillette and Baker (Colorado).*Paracoelidia* Baker.1898, *Canad. Ent.* 30 : 292.Type—*Paracoelidia tuberculata* Baker (North America).*Salvina* Melichar.1926, *Ann. Mus. Nat. Hung.* 23 : 344.Type—*Tettigonia dorsignata* Fowler (Panama).*Taxonomic Notes.*

The genera comprised in this sub-family, though usually referred to the COELIDIINAE (JASSINAE), have, for a long time, been recognised as having distinctive characteristics. Thus Osborn (1897) referred to *Neocoelidia tumidifrons* as "an unusual species which suggests relationship between *Euacanthus* and *Xestocephalus*." Recently (1943) Oman created the sub-family NEOCOELIDIINAE to receive this group of genera.

Discussion of the NEOCOELIDIINAE.

Leaf-hoppers in this sub-family have a certain superficial resemblance to both the COELIDIINAE and the NIRVANINAE, but an analysis of their basic characters provides no indication of any real relationship to either of these sub-families. It is of interest to note the manner in which the antennal ledges have come to lie alongside the frontal sutures in certain forms and to compare fig. 25a, c, e with fig. 17m, where these ledges are situated in such a very different position.

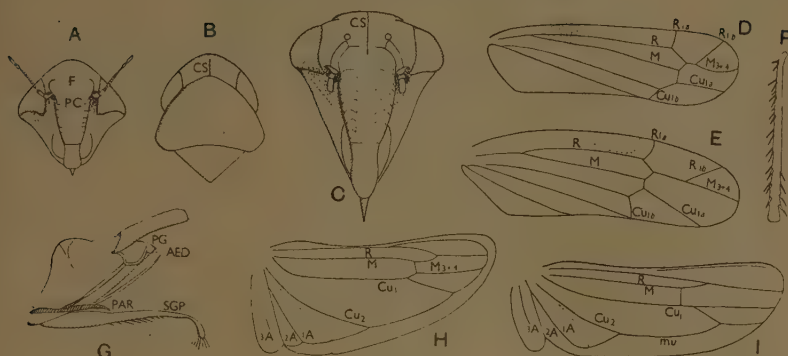
TYPHLOCYBINAE (fig. 26).

Distribution.

Universal.

Size, Coloration and General Appearance.

The TYPHLOCYBINAE are small, narrow, delicate leaf-hoppers which range in size from 2 to 4 mm. In colour they are mostly yellow, or green, but they may also be red, or whitish, and sometimes they display a colour-pattern development.



26

FIG. 26.

A, *Typhlocyba 10-punctata* Fall, head; B, *T. 10-punctata*, head and thorax, dorsal aspect; C, *Empoasca* sp., head; D, *Alconeura tricolor* Van Duzee, tegmen; E, *Typhlocyba 10-punctata*, tegmen; F, *Dikraneura cockerelli* Gill, hind tibia; G, *Empoasca quadripunctata* Ev., male genitalia; H, *Alconeura tricolor*, wing; I, *Erythroneura comes* Say, wing.

Food-plants and Habits.

Several species are injurious, hence numerous food-plant records are available (e.g., Poos and Wheeler, 1943), and while it is probable that the greater number is arboreal, many are also associated with herbaceous plants; a few species, which are double-brooded, breed on different plants for each generation (e.g., *Typhlocyba rosae* L., Ball, 1920).

Description.

Head. The face is usually long and narrow, but it may also be wider than long; the labium is of variable length and the maxillary plates are narrow. The frons, which is seldom separated from the post-clypeus, is always on the face of the head, and frontal and post-frontal sutures are sometimes retained. In a few species the coronal suture extends on to the frons, but this is a secondary development and of no structural significance. Even when no trace remains of an epistomal suture, the cibarial muscles seldom encroach on to the frons. The antennae usually are long, the antennal depressions deep and the antennal ledges, which are short and variable in position, may be in line with the anterior corners of the eyes. Ocelli, if present, are on the face, but in those species in which the face and the crown form one curved surface, they are visible also from above. The crown, which is usually of equal width to the eyes, may be medially produced.

Thorax. The pronotum, which is narrow laterally and widest posteriorly, is occasionally pitted.

Legs. The fore and middle tibiae are rounded, and the hind tibiae are long and slender and bear long, delicate spines.

Tegmina. The tegmina, which are long and narrow and lack an appendix (except in *Alebra* and related genera), usually have an oval wax-like plaque in the costal region. The venation is considerably reduced, and as well as R_s and M_{1+2} being invariably absent, several cross-veins are lacking and the anal veins are seldom distinguishable.

Wings. The venation of the wings is also reduced and the marginal vein may be either partially or completely absent.

Genera comprised in the TYPHLOCYBINAÆ.

Aguriahana Distant (synonym of *Eupteryx* Curtis).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 105.

Type—*Aguriahana metallica* Distant (North-east India).

Aidola Melichar (synonym of *Erythroneura* Fitch).

1914, *Notes Mus. Leiden* 36 : 142.

Type—*Typhlocyba orbata* Melichar (Ceylon).

Akotettix Matsumura.

1931, *Ins. Mats.* 6 : 77.

Type—*Akotettix akonis* Matsumura (Formosa).

Alconeura Ball and De Long.

1925, *Ann. Soc. ent. Amer.* 18 : 324.

Type—*Alconeura rotundata* Ball and De Long (North America).

Alebra Fieber (new name for *Compsus* Fieber).

1872, *Kat. Eur. Cicadinen* : 14.

Alebroides Matsumura.

1931, *Ins. Mats.* 6 : 68.

Type—*Alebroides marginatus* Matsumura (Formosa).

Aneono Kirkaldy.

1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 358.

Type—*Aneono pulcherrima* Kirkaldy (New South Wales).

Anomia Fieber (synonym of *Typhlocyba* Germar).

1866, *Verh. zool. bot. Ges. Wien.* 16 : 509.

Type—*Cicada quercus* Fabricius.

Aphanalebra McAtee.

1926, *J. N. Y. ent. Soc.* 34 : 147.

Type—*Protalebra unipuncta* Baker (Brazil).

Apheliona Kirkaldy.

1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 67.

Type—*Heliona biocula* Kirkaldy (= *bioculata* Melichar) (Ceylon).

Bolanusoides Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 90.

Type—*Bolanusoides heros* Distant (North-West India).

Camulus Distant (synonym of *Bolanusoides* Distant).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 97.

Type—*Camulus ornatus* Distant (Northern India).

Chikkaballapura Distant (synonym of *Empoanara* Distant).

1918, *Faun. Brit. Ind. Rhyn.* 7 : 107.

Type—*Chikkaballapura maculosa* Distant (India).

Chloria Fieber (synonym of *Empoasca* Walsh).

1866, *Verh. zool.-bot. Ges. Wien.* 16 : 508.

Type—*Cicadula viridula* Fallen (Oshanin, 1918) (Sweden).

Chlorita Fieber (new name for *Chloria* Fieber).

1872, *Kat. Eur. Cicadinen* : 14.

Chloroneura Walsh (synonym of *Dikraneura* Hardy).

1864, *Proc. Boston Soc. nat. Hist.* 9 : 316.

Type—*Chloroneura abnormis* Walsh (North America).

Cicadella Dumeril.

1806, *Zool. Analyst.* Paris ed. : 266.

Type—*Cicada vittata* Linnaeus (Europe).

Compsus Fieber (preoccupied, see *Alebra* Fieber).

1866, *Verh. zool. bot. Ges. Wien.* 16 : 507.

Type—*Cicada albostriella* Fallen (= *elegantula* Zett. = *discicollis* H.S.) (Sweden).

- Conometopus* Motschulsky (preoccupied, see *Motchulskyia* Kirkaldy).
1863, *Bull. Soc. Nat. Mosc.* 36 : 103.
Type—*Conometopus inspiratus* Motschulsky (Mt. Patannas).
- Cybus* Douglas and Scott (invalid emendation of *Kybos* Fieber).
1875, *Ent. mon. Mag.* 12 : 26.
- Dialecticopteryx* Kirkaldy.
1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 71.
Type—*Dialecticopteryx australica* Kirkaldy (Queensland).
- Dicraneura* Puton (invalid emendation of *Dikraneura* Hardy).
1886, *Cat. Hemipt.* : 86.
- Dicraneura* Woodworth (invalid emendation of *Dikraneura* Hardy).
1888, *Psyche* 5 : 75.
- Dicranoneura* Douglas (synonym of *Dikraneura* Hardy).
1875, *Ent. mon. Mag.* 12 : 27.
Type—*Cicadula citrinella* Zetterstedt (Lappland).
- Dikraneura* Hardy.
1850, *Trans. Tyneside Nat. Fld. Club* 1 : 423.
Type—*Dikraneura variata* Hardy (England).
- Dikraneuroidea* Lawson.
1929, *Bull. Brooklyn ent. Soc.* 24 : 307.
Type—*Dikraneuroidea beameri* Lawson (Texas).
- Diomma* Motschulsky (synonym of *Eupteryx* Curtis).
1863, *Bull. Soc. Nat. Mosc.* 36 : 102.
Type—*Diomma ochracea* Motschulsky (Ceylon).
- Edwardsiana* Jazykov (Zachvatkin) (synonym of *Typhlocyba* Germar).
1929, *Rev. russe Ent.* 23 : 265 (no description).
Type—*Edwardsiana ruthenica* Jazykov (Russia).
- Empoa* Fitch (synonym of *Typhlocyba* Germar).
1851, *Fourth Rep. Regents Univ. N.Y. on State Cabinet Nat. Hist.* : 68.
Type—*Empoa querci* Fitch (North America).
- Empoanara* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 106.
Type—*Empoanara militaris* Distant (India).
- Empoasca* Walsh.
1862, *Prairie Farmer* 10 : 148, 149 (Sept.).
1864, *Proc. Boston Soc. nat. Hist.* 9 : 315.
Type—*Empoasca viridiscens* Walsh (Distant, 1908) (North America).
- Empoascanara* Distant (synonym of *Erythroneura* Fitch).
1918, *Faun. Brit. Ind.* 7 : 94.
Type—*Empoascanara prima* Distant (South India).
- Erythria* Fieber (synonym of *Dikraneura* Hardy).
1866, *Verh. zool.-bot. Ges. Wien.* 16 : 507.
Type—*Cicada aureola* Fallen (Sweden).
- Erythridea* Ribaut.
1936, *Faune de France*, 31 : 223.
Type—*Deltocephalus ferrari* Puton (Europe).
- Erythroneura* Fitch.
1851, *Rep. N. Y. State Mus.* : 62.
Type—*Erythroneura tricineta* Fitch (Oshanin, 1912) (North America).
- Eualebra* Baker.
1899, *Psyche* 8 : 402.
Type—*Eualebra smithii* Baker (Brazil).

- Eupteryx* Curtis (synonym of *Cicadella* Dumeril).
1833, *Ent. Mag.* 1 : 192 (Jan.).
Type—*Cicada picta* Fabricius (= *Cicada atropunctata* Goeze) (Germany).
- Eurhadina* Haupt (synonym of *Eupteryx* Curtis).
1929, *Zool. Jb.* 58 : 269.
Type—*Cicada pulchella* Fallen (Sweden).
- Eutambourina* Evans.
1942, *Pap. Roy. Soc. Tasm.* 1941 : 27.
Type—*Eutambourina punctata* Evans (Queensland).
- Forcipata* De Long and Caldwell.
1936, *Ann. ent. Soc. Amer.* 29 : 70
Type—*Forcipata loca* De Long and Caldwell (North America)
- Hebata* De Long.
1931, *Tech. Bull. U.S. Dept. Agric.* 231 : 32.
Type—*Empoasca nigra* Gillette and Baker (North America).
- Heliona* Melichar.
1903, *Homopt. Faun. Ceylon* : 215.
Type—*Heliona constricta* Melichar (Distant, 1908) (Ceylon).
- Helionides* Matsumura.
1931, *Ins. Mats.* 6 : 79.
Type—*Helionides singularis* Matsumura (Japan).
- Hirolettix* Matsumura.
1931, *Ins. Mats.* 6 : 59, 64 (1931), 102 (1932).
Type—*Hirolettix arisanellus* Matsumura (Formosa).
- Homa* Distant.
1908, *Faun. Brit. Ind. Rhyn.* 4 : 400.
Type—*Homa insignis* Distant (Ceylon).
- Hybla* McAtee.
1932, *J. Dept. Agric. Porto Rico* 16 : 119, 120.
Type—*Hybla maculata* McAtee (Porto Rico).
- Hylodea* McAtee.
1926, *J.N.Y. ent. Soc.* 34 : 158.
Type—*Hylodea depressa* McAtee (Porto Rico).
- Hymettia* McAtee.
1919, *Proc. biol. Soc. Wash.* 32 : 121.
Type—*Tettigonia trifasciata* Say (North America).
- Idia* Fieber (preoccupied, see *Zyginidia* Haupt) (synonym of *Erythroneura* Fitch).
1866, *Verh. zool.-bot. Ges. Wien.* 16 : 509.
Type—*Typhlocyba scutellaris* Herrich Schaffer (Europe).
- Idona* De Long.
1931, *Tech. Bull. U.S. Dept. Agric.* 231 : 50.
Type—*Empoasca minuenda* Ball (North America).
- Igutettix* Matsumura.
1931, *Ins. Mats.* 6 : 64 (1931), 105 (1932).
Type—*Igutettix pulverosus* Matsumura (Japan).
- Joruma* McAtee.
1924, *Florida Entomologist* 8 : 34.
Type—*Joruma picea* McAtee (North America).
- Kahaono* Kirkaldy.
1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 361.
Type—*Kahaono hanuala* Kirkaldy (Queensland).

Kallebra McAtee.1926, *J.N.Y. ent. Soc.* **34** : 147.Type—*Protalebra ninettae* Baker (Brazil).*Kybos* Fieber (synonym of *Empoasca* Walsh).1866, *Verh. zool.-bot. Ges. Wien.* **16** : 508.Type—*Cicada smaragdula* Fallen (Europe).*Liguropia* Haupt (synonym of *Dikraneura* Hardy).1930, *Mitt. Dtsch. ent. Ges. Jg.* **1** : 156.Type—*Liguropia menozzi* Haupt (Italy).*Molopopterus* Jacobi.1910, *Sjöstedt Kilimandjaro Meru Exp.* **12** : 183.Type—*Molopopterus nigriplaga* Jacobi (East Africa).*Motschulskyia* Kirkaldy (new name for *Conometopus* Motsch.).1905, *Wien. ent. Zeit.* **24** : 266.*Naratettix* Matsumura.1931, *Ins. Mats.* **6** : 73.Type—*Erythria zonata* Matsumura (Japan).*Nesopteryx* Matsumura.1931, *Ins. Mats.* **6** : 60, 64, 102.Type—*Nesopteryx arisana* Matsumura (Formosa).*Nikkotettix* Matsumura.1931, *Ins. Mats.* **6** : 76.Type—*Nikkotettix galolisi* (galloisi) Matsumura (Japan).*Notus* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* **16** : 31, 58.Type—*Notus flavipennis* Zetterstedt (Europe).*Paralebra* McAtee.1926, *J.N.Y. ent. Soc.* **34** : 147.Type—*Protalebra similis* Baker (Brazil).*Parallaxis* McAtee.1926, *J.N.Y. ent. Soc.* **34** : 154.Type—*Parallaxis vacillans* McAtee (Brazil).*Plagalebra* McAtee.1926, *J.N.Y. ent. Soc.* **34** : 147.Type—*Protalebra singularis* Baker (Brazil).*Platycyba* Matsumura.1931, *Ins. Mats.* **6** : 60 (1931), 103 (1932).Type—*Platycyba bistriata* Matsumura (Japan).*Platyettix* Matsumura.1931, *Ins. Mats.* **6** : 59, 64 (1931), 104 (1932).Type—*Motschulskia pulchra* Matsumura (1916) (Japan).*Protalebra* Baker.1899, *Psyche* **8** : 402.Type—*Alebra curvilinea* Gillette (Brazil).*Pyramidotettix* Matsumura.1931, *Ins. Mats.* **6** : 59, 64 (1931), 104 (1932).Type—*Conometopus citri* Matsumura (Formosa).*Sacapome* Schumacher.1915, *Suppl. Ent.* : 127.Type—*Sacapome formosana* Schumacher (Formosa).*Sajitettix* Matsumura.1931, *Ins. Mats.* **6** : 76.Type—*Sajitettix ferrugineus* Matsumura (Japan).

- Shaddai* Distant (synonym of *Alebra* Fieber).
 1918, *Faun. Brit. Ind. Rhyn.* 7 : 15.
 Type—*Shaddai typicus* Distant (India).
- Sinalebra* Zachvatkin.
 1936, *Ark. Zool.* 29 (A) : 4 : 16.
 Type—*Sinalebra hummeli* Zachvatkin (China).
- Sirosoma* McAtee.
 1933, *Philipp. J. Sci.* 51 : 545.
 Type—*Sirosoma hiaticula* McAtee.
- Togaricrania* Matsumura.
 1931, *Ins. Mats.* 6 : 72.
 Type—*Togaricrania rubrovitta* Matsumura (Japan).
- Togaritettix* Matsumura.
 1931, *Ins. Mats.* 6 : 71.
 Type—*Togaritettix serratus* Matsumura (Japan).
- Typhlocyba* Germar.
 1833, *Silb. Rev. Ent.* 1 : 180 (Sept.).
 Type—*Cicada quercus* Fabricius (Woodworth, 1889) (Germany).
- Typhlocybella* Baker.
 1903, *Invert. Pacif.* 1 : 3.
 Type—*Typhlocybella minima* Baker (Nicaragua).
- Zygina* Fieber (synonym of *Erythroneura* Fitch).
 1866, *Verh. zool.-bot. Ges. Wien.* 16 : 509.
 Type—*Typhlocyba nivea* Mulsant (France).
- Zyginella* P. Löw (synonym of *Typhlocyba* Germar).
 1885, *Verh. zool.-bot. Ges. Wien.* 35 : 346.
 Type—*Zyginella pulchra* Löw (Austria).
- Zyginidia* Haupt (new name for *Idia* Fieber).
 1929, *Zool. Jb.* 58 : 268.
- Zyginoides* Matsumura.
 1931, *Ins. Mats.* 6 : 59, 64 (1931), 106 (1932).
 Type—*Eupteryx taiwanus* Shiraki (1910) (Formosa).

Taxonomic Notes.

The TYPHLOCYBINAE, which have long been recognised as a distinct and well-defined group of leaf-hoppers, have either in the past been regarded as a tribe of the JASSINAE (Lawson, 1920), as a sub-family of the JASSIDAE (Kirkaldy, 1906), or they have been given family status (Haupt, 1929); they have even been recognised as a group of equivalent rank with the CERCOPIDAE (Ribaut, 1936). McAtee (1934), followed by Oman (1943), recognised the following tribes: Alebrini, Dikraneurini, Jorumini and Cicadellini. I have refrained from following these authors in the use of these tribes because my own present knowledge of this sub-family is insufficient to enable me to assess their merits. McAtee (1934) removed *Bolanusoides* and *Camulus* from the TYPHLOCYBINAE and referred them to the NIRVANINAE, but I have replaced them since both are related to *Aneono* and are most certainly true representatives of the TYPHLOCYBINAE. In spite of the very distinctive characters of this group, several of the genera have at times been placed in incorrect sub-families, as for instance *Shaddai*, which Distant referred to the TETTIGONIELLINAE. Some authors use the group name EUPTERYGINAE

instead of TYPHLOCYBINAE. Mr. China has drawn my attention to the fact that not only is the latter the oldest group name, having been used by J. Sahlberg in 1871, but that *Typhlocyba* is the older genus.

Discussion of the TYPHLOCYBINAE.

The position of the TYPHLOCYBINAE with respect to the rest of the JASSIDAE has been discussed by several authors. Gillette (1898) believed that they were the lowest representatives of the family and Lawson (1920) that they were the highest; Kirkaldy (1906) considered them to be a natural development of the Macrostelini Tetigoniids. My own opinion is that they lie close to the base of the jassid stem, and that they are neither derivatives of, nor ancestral to, any other present-day group of leaf-hoppers. Their primitive features include their small size, the structure of their heads and their occasional pitted appearance; the reduction of the venation of the tegmen is evidently an early specialisation. George (1933) and Ribaut (1936) have recorded the presence of sound-producing organs in these insects which are apparently especially associated with the males. These structures may either be a secondary development, or else they may represent the retention of an ancestral character (see Pt. 2, 1946, *Trans. R. ent. Soc. Lond.* 97 : 42.)

Certain representatives of this sub-family (e.g., *Aneono*, *Bolanusoides*) superficially resemble Nirvanids. They are considerably flattened insects with a short labium and lack a transverse clypeal suture. They also have deep antennal depressions, which are situated at the hind margin of the face on either side of a completely ventral frons. Their true position can be determined by the characteristic venation of their tegmina, which have an oval wax plate in the costal area; in addition these leaf-hoppers lack ocelli, a character shared with several other genera of the TYPHLOCYBINAE but quite unknown in the NIRVANINAE.

TARTESSINAE (fig. 27).

Distribution.

Australia and the Oriental region.

Size, Coloration and General Appearance.

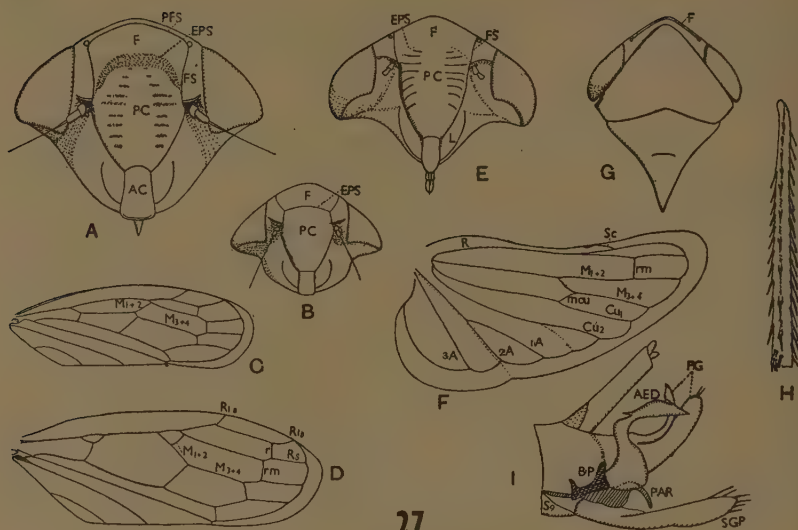
The TARTESSINAE range in length from 5-10 mm., and in colour they are either brown or black, sometimes with a thorax which is pale yellow, or pale green, or they may be entirely pale green.

Food-plants and Habits.

They are essentially arboreal leaf-hoppers, which in Australia live on eucalypts; in Formosa *Tartessus ferrugineus* Walker has been taken on fig and orange trees (Schumacher, 1915).

Description.

Head. The labium is of variable length, the ante-clypeus is completely separated from the post-clypeus and the maxillary plates are usually wide. The post-clypeus, which is



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FIG. 27.

A, *Tartessus fulvus* Walk., head; B, *Tartessus ferrugineus* Walk., head; C, *T. ferrugineus*, tegmen; D, *Sarpestus bistrigia* Walk., tegmen; E, *Tartessella attenuata* Ev., head; F, *Tartessus fulvus*, wing; G, *Tartessus ferrugineus*, head and thorax, dorsal aspect; H, *Tartessus fulvus*, hind tibia; I, *Tartessus idyia* Kirk., male genitalia.

flat, only encroaches on to the anterior part of the frons, from which it is often separated by either a distinct, or else a vestigial, epistomal suture. The frons, which is extensive, is usually rectangular in shape and entirely facial in position, although it may be narrowly visible from above, and both frontal and postfrontal sutures are generally retained. The antennae, which are usually nearer to the anterior than to the posterior corners of the eyes, are of medium length; the antennal ledges are transverse and the antennal depressions shallow; in some forms long delicate setae arise from the proximal segments of the flagellum. The crown, which is usually narrow, is generally separated from the face by a marginal carina which replaces the postfrontal sutures and which may extend laterally as far as the eyes, posterior to the ocelli. In forms with narrowly produced heads (*Stenotartessus*), this carina forms an inverted V on the crown, close to its anterior margin. The ocelli, which may be either ventral, marginal, or dorsal in position, are always close to the apices of the frontal sutures and the eyes are large.

Thorax. The pronotum, which is narrow laterally, is heart-shaped and flat, and the scutellum is large.

Legs. The fore and middle tibiae are rounded, and the hind tibiae, which are long and slender, have a dense armature of long spines, and a few minute spines occur between each of the enlarged bases of the strongest spines.

Tegmina. The tegmina, which are hyaline, are usually broad and have a wide apical appendix; but they may also be narrow apically and have a narrow appendix. The venation is usually complete, but in *Sarpestus* spp. the proximal part of M is lacking. The veins sometimes bear small hairs, and often two or three short bristles occur at the distal apex of the anal border.

Wings. The marginal vein continues on to the anal area.

Genera comprised in the TARTESSINAE.

Borduria Distant.1908, *Rec. Ind. Mus.* 2 : 147.Type—*Bythoscopus impressa* Walker (Batchian).*Euprora* Evans (preoccupied, see *Stenotartessus* Evans).1939, *Pap. Roy. Soc. Tasm.* 1938 : 9.Type—*Euprora mullensis* Evans (Western Australia).*Newmaniana* Evans.1942, *Trans. Roy. Soc. W. Australia* 27 : 152.Type—*Newmaniana viridis* Evans (Western Australia).*Sarpestus* Spånberg.1877, *Öfvers Vetens-Akad. Förh. Stockh.* 34 : 11.Type—*Sarpestus specularis* Spånberg (Mysol).*Stenotartessus* (nom. nov. pro *Euprora* Evans, 1939, not *Euprora* Busck., 1906 (Lep.))*Tartessella* Evans.1937, *Pap. Roy. Soc. Tasm.* 1936 : 56.Type—*Tartessella attenuata* Evans (Western Australia).*Tartessoides* Evans.1937, *Pap. Roy. Soc. Tasm.* 1936 : 55.Type—*Tartessoides griseus* Evans (Western Australia).*Tartessus* Stål.1865, *Öfvers. Vetens-Akad. Förh. Stockh.* 22 : 156.Type—*Bythoscopus malayus* Stål (= *ferrugineus* Walker) (Malaya).

Taxonomic Notes.

Tartessus was placed in the Phrynomorphini by Kirkaldy (1907), and by Distant (1908) in the Tartessusaria, a tribe in which he included also several unrelated genera. Oshanin (1912) referred this genus to the Acocephalini and Baker (1919) associated it with *Macroceps*, *Thymbris* and *Putoniessa* in the Tartessusaria. Haupt (1929) placed it in the EUSCELIDAE, and in 1939b I created a family, the TARTESSIDAE, to comprise this group of genera. The genera *Newmaniana* and *Stenotartessus* I have formerly considered as thymbrids.

Discussion of the TARTESSINAE.

In some representatives of this sub-family the antennae lie closer to the posterior, than to the anterior, corners of the eyes, and in build these leaf-hoppers are more robust than those comprised in the previous eight sub-families. It is thus with some hesitation that I am including them in the Macropsides instead of the Ulopides and at present I can make no suggestions as to their relationship to other jassids.

Most jassids which occur in Australia as well as in the Oriental region will have entered Australia from the north. The TARTESSINAE, on the other hand, most probably spread into Asia from a Western Australian source. Their origin therefore possibly precedes that of the Thymbrini, an Australian group which is associated especially with Eastern Australia.

JASSINAE.¹³

The jassids which were formerly associated with *Jassus* (*Bythoscopus*)¹³ in the sub-family BYTHOSCOPINAE¹³ comprised the genera *Agallia*, *Idiocerus* and *Macropsis* and their relatives, as well as several other genera added from time to time by various authors.

In earlier papers (1939b, 1941) I have presented a different concept of this sub-family which I now propose to modify by the removal of certain genera and the addition of others. I am of the opinion that all the several genera comprised in my present concept of the group have been derived from some early *Jassus*-like form, although not from species which could be referred to the genus *Jassus*. This hypothetical ancestor will have possessed the following features: lora which did not extend as far as the margin of the head and wide maxillary plates; wide transverse antennal ledges in alignment with a transverse epistomal suture and the anterior corners of the eyes; a rectangular facial frons, somewhat wider than the post-clypeus, and ventral ocelli situated close to the posterior corners of the frons; a crown no wider than the width of the eyes and forming a continuous curved surface with the face; wide propleurae separating the eyes from the bases of the tegmina, and a pronotum wider posteriorly than anteriorly and with the hind margin parallel to the anterior margin; tegmina with complete jassid venation and a wide appendix; male genitalia with the sternite of the ninth segment distinct from the tergite; wide flap-like pygophores bearing spines externally and a simple curved dorsally directed aedeagus.

With the encroachment of the post-clypeus on to the region of the frons, the epistomal suture becomes arched and the antennal ledges oblique and their apparent overlap on to the fronto-clypeus becomes accentuated. In some forms the backward extension of the post-clypeus accompanied by the antennae results in the restriction of the frons to a small narrow facial border and the ocelli in consequence become marginal and finally dorsal in position (Gyponini). In others, the flexing of the head across the axis of the antennal ledges results in all that part of the head which lies posterior to the antennae becoming the crown of the head, and in this way also the ocelli may come to assume a dorsal position (Penthimiini, Trocnadini). Forms also occur in which the head has later become flattened and produced and hence ledrine in appearance (e.g., *Thaumatoscopus*).

In view of the instability of structure which is such a feature of this sub-family, a precise definition of even its principal characteristics is an impossibility, but a study of the accompanying illustrations should enable its representatives to be recognised. I propose to divide the sub-family into seven tribes, the Penthimiini, Krisnini, Gyponini, Selenocephalini, Jassini, Trocnadini and Reuterellini.

¹³China and Fennah, 1946, have, on nomenclatorial grounds, ascribed the leaf-hopper, so long known as *Bythoscopus lanio* L., to the genus *Jassus* Fabricius, of which it is the type.

Penthimiini (fig. 28).

Distribution.

The Penthimiini occur in all the principal geographical regions, and though their headquarters would appear to be in the Oriental region, they are also well represented in South Africa and in Queensland.

Size, Coloration and General Appearance.

They range in length from 3 to 10 mm. and in colour they are either black, reddish-brown or pale sandy brown, or they may have a black and white pattern development. In shape they are somewhat flattened and the larger species, which have their tegmina steeply overlapping apically, are somewhat cercopoid in appearance.

Food-plants and Habits.

In North America *Penthimia americana* Fitch occurs on oak, and on hickory and other shrubs (De Long, 1916; Van Duzee, 1923); *P. theae* Matsumura feeds on tea in Formosa (Schumacher, 1915), and *P. nigra* Goeze feeds on *Eunonymus* in Europe (Haupt, 1935).

Description.

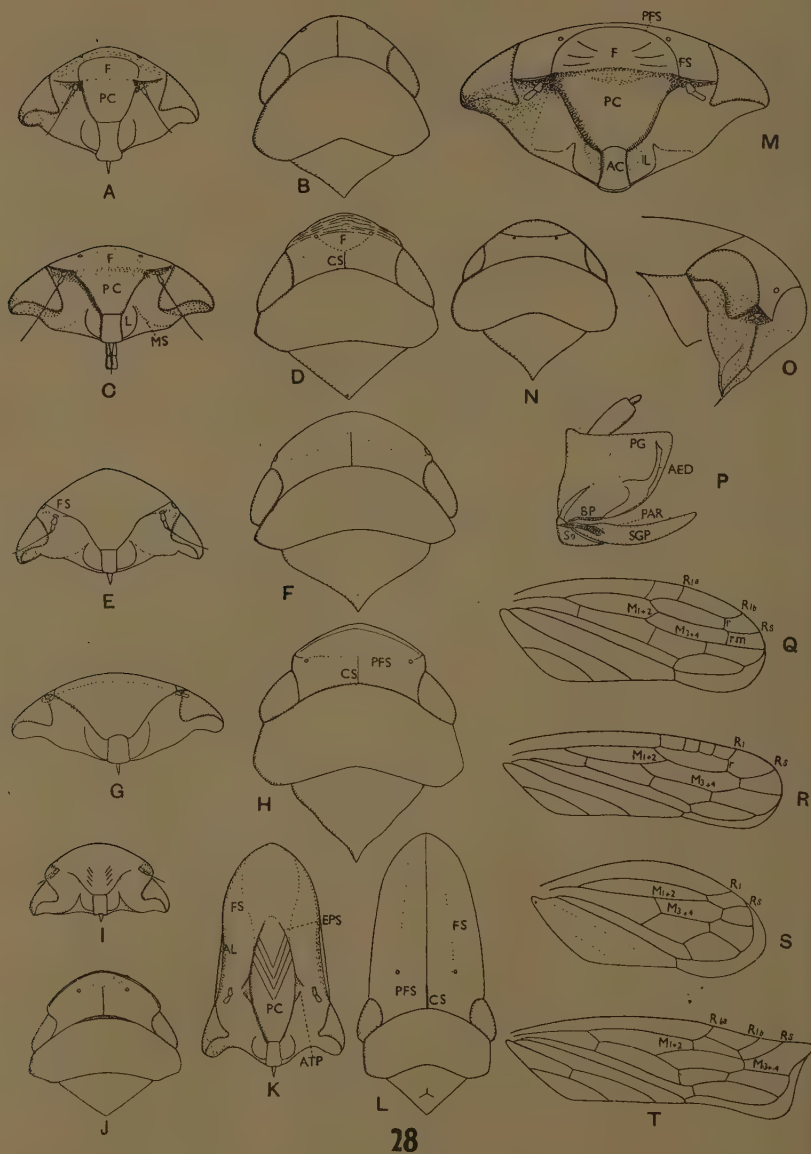
Head. The head, which is variable in shape, is usually wider than long. The labium is short, the maxillary plates wide and the lora extend almost as far as the margins of the maxillary plates. The antennae are variable in length and the antennal ledges which extend on to the post-clypeus are usually narrowly prominent but may be absent. The remainder of the head may (a) have a distinct rectangular frons with or without a vestigial epistomal suture, and ocelli situated on the thickened, but not rim-like, anterior margin of a well-developed flat crown. (fig. 28a, b): (b) have a declivous crown which forms one curved surface as far as the antennal ledges; in consequence the frons and the ocelli lie on the crown and the frontal and postfrontal sutures, if retained, form a semicircle (fig. 28c, d, m, n, o): (c) be wide and flat, both dorsally and ventrally, with the antennal ledges either partially or completely obliterated; the frontal sutures, which are on the face, directed laterally towards the eyes and the frons and ocelli on the crown; the crown separated from the face by a thickened margin and the ocelli close to the anterior corners of the crown (fig. 28e, f, g, h): (d) have the anterior margin of the crown foliaceous and produced to a varying degree with the antennal ledges and the epistomal suture either retained or obliterated; the frontal sutures on the face and directed posteriorly (in short-headed forms) or else on the crown, when that part of the crown, anterior to the ocelli, is elongate, (fig. 28i, j, k, l).

Thorax. The pronotum is usually wide laterally and may be slightly declivous; sometimes it is collar-like, but more often it is widest posteriorly and the fore and hind margins are parallel with each other.

Legs. The fore and middle tibiae may be rounded, flattened, or quadrilateral in section. The hind tibiae, which are curved and flattened, bear two or three rows of long, strong spines, and they may also have additional small spines, set either between the large spines, or between the rows of large spines.

Tegmina. The tegmina, which are variable in shape, but most frequently rounded apically with a wide appendix, have usually a steep apical overlap; this may involve the cell between the arms of Cu_1 as well as the appendix. The venation is sometimes complete and often additional cross-veins occur in the costal area.

Male Genitalia. The ninth sternite is distinct, the parameres are short and the subgenital plates, which are broad, narrow apically.



Genera comprised in the *Penthimiini*.*Amberbakkia* Distant.1912, *Ann. Mag. nat. Hist.* (8) 10 : 443.Type—*Petaloecephala specularia* Walker (New Guinea).*Auropenthimia* Evans.1947, *Trans. R. ent. Soc. Lond.* 98 : 255.Type—*Auropenthimia aburensis* Evans (West Africa).*Betsileonas* Kirkaldy (new name for *Thaumastus* Stål).1903, *Wien. ent. Zeit.* 22 : 13.*Ectopiocephalus* Kirkaldy (synonym of *Penthimia* Germar).1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 463.Type—*Ectopiocephalus vanduzeei* Kirkaldy (Queensland).*Eovulturnops* Evans.1947, *Trans. R. ent. Soc. Lond.* 98 : 255.Type—*Eovulturnops selenocephaloides* Evans (British Guiana).*Haranga* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 248.Type—*Penthimia orientalis* Walker (unknown, ? N. India).*Jafar* Kirkaldy (new name for *Setabis* Stål).1903, *Wien. ent. Zeit.* 22 : 13.*Kronos* Distant.1917, *Trans. Linn. Soc. London (Zool.)* (2) 17 : 307.Type—*Kronos typicus* Distant (Seychelles).*Ledroides* Dammerman.1910, *Notes Mus. Leiden* 33 : 59.Type—*Ledroides reticulata* Biermann (Sumatra).*Malichus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 24.Type—*Malichus capitatus* Distant (Ceylon).*Neodartus* Melichar.1903, *Homopt. Faun. Ceylon* : 162.Type—*Neodartus acocephaloides* Melichar (Ceylon).*Neovulturnus* Evans.1937, *Mem. Queensland Mus.* 11 : 150.Type—*Vulturnus vanduzeei* Kirkaldy (Queensland).*Penthimia* Germar.1821, *Mag. Ent.* 4 : 46.Type—*Cicada nigra* Goeze (South Europe).*Penthimidia* Haglund.1899, *Öfvers Vetens-Akad. Förh. Stockh.* 1899 : 55.Type—*Penthimidia exima* Haglund (Cameroons).

FIG. 28.

A, *Thaumatooides caffra* Ev., head ; B, *T. caffra*, head and thorax, dorsal aspect ; C, *Neovulturnus maculosus* Ev., head ; D, *N. maculosus*, head and thorax, dorsal aspect ; E, *Eovulturnops selenocephaloides* Ev., head ; F, *E. selenocephaloides*, head and thorax, dorsal aspect ; G, *Auropenthimia aburensis* Ev., head ; H, *A. aburensis*, head and thorax, dorsal aspect ; I, *Vulturnus virgidemia* Kirk., head ; J, *V. virgidemia*, head and thorax, dorsal aspect ; K, *Platyscopus badius* Ev., head ; L, *P. badius*, head and thorax, dorsal aspect ; M, *Penthimia vanduzeei* Kirk., head ; N, *Penthimia atra* Fabr., head and thorax, dorsal aspect ; O, *Penthimia maculata* Ev., head in profile ; P, *Penthimia vanduzeei*, male genitalia ; Q, *P. vanduzeei*, tegmen ; R, *Platyscopus badius*, tegmen ; S, *Penthimia atra*, tegmen ; T, *Auropenthimia aburensis*, tegmen.

Platyscopus Evans.1943, *Trans. Roy. Soc. W. Aust.* 27 : 145.Type—*Platyscopus badius* Evans (Western Australia).*Setabis* Stål (preoccupied, see *Jafar* Kirkaldy).1866, *Hemipt. Africana* 4 : 111.Type—*Gypona javeti* Signoret (Calabar).*Tambila* Distant.1907, *Faun. Brit. Ind. Rhyn.* 4 : 247.Type—*Tambila greeni* 1 instant (Ceylon).*Thaumastus* Stål (preoccupied, see *Betsileonas* Kirkaldy).1864, *Ann. Soc. ent. Fr.* 4 : 67.Type—*Ledra marmorata* Blanchard (Madagascar).*Thaumatotopoides* Evans.1947, *Trans. R. ent. Lond.* 98 : 255.Type—*Thaumatotopoides caffra* Evans (South-West Africa).*Thaumatoscopus* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 462.Type—*Thaumatoscopus galeatus* Kirkaldy (Queensland).*Uzelina* Melichar.1903, *Homopt. Faun. Ceylon* : 181.Type—*Uzelina laticeps* Melichar (Ceylon).*Vulturnus* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 463.Type—*Vulturnus vulturnus* Kirkaldy (Queensland).*Taxonomic Notes.*

Penthimia has formerly been referred to the TETTIGONIELLINAE (Melichar, 1903), to the JASSINAE, *Penthimaria* (Oshanin, 1912), and to the GYPONINAE (Lawson, 1920 ; Haupt, 1929 ; Merino, 1936 ; Oman, 1943). Kirkaldy (1907), who recognised a tribe, the Penthimiini, referred to it such unrelated genera as *Signoretia*, *Chiasmus* and *Errhomenellus*. *Thaumatoscopus*, which Kirkaldy placed in the PENTHIMIINAE and Haupt in the LEDRIDAE, was recognised by Baker (1923) as the type of a new family, the THAUMATOSCOPIIDAE, but even though species in this genus differ widely from those comprised in *Penthimia*, the two genera are linked by a complete series of gradations (Evans, 1937c).

Krisnini (fig. 29).*Distribution.*

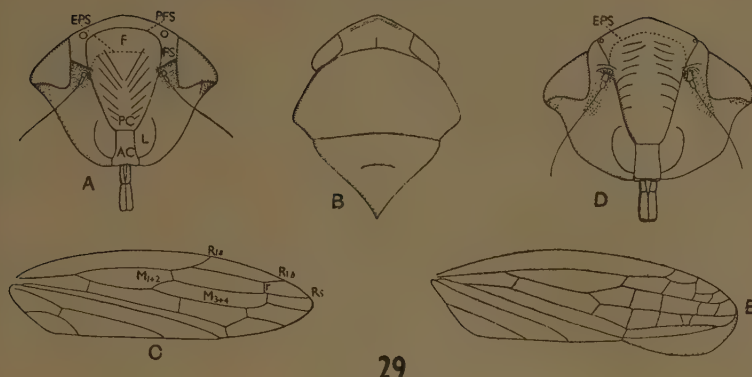
The Oriental region, Madagascar, Africa and Porto Rico.

Size, Coloration and General Appearance.

The *Krisnini* range from 8 to 12 mm. in length and in colour they are either brown, green, whitish or orange, and lack any pattern development. In appearance they are either long and narrow with tectiform tegmina, or else they are broad and flattened.

Food-plants and Habits.

Apparently unknown.



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FIG. 29.

A, *Krisna striata* Kirby, head; B, *K. striata*, head and thorax, dorsal aspect; C, *Acropona gardineri* Dist., tegmen; D, *A. gardineri*, head; E, *Krisna olivaceus* Walk., tegmen.

Description.

Head. The face is flat or slightly convex and the labium is short or of moderate length. The ante-clypeus, which narrows posteriorly, is sometimes continuous with the post-clypeus. The maxillary plates are wide and the lora sometimes do not continue as far as their outer margins. The frons, which is sometimes separated from the post-clypeus by a distinct epistomal suture, is entirely facial in position and the postfrontal sutures, if retained, form part of the hind margin of the face. The antennae are long, the antennal depressions of variable depth and the antennal ledges are oblique, antero-medially directed, and nearer to the posterior than to the anterior corners of the eyes. The ocelli lie close to the apices of the frontal sutures and may be either ventral or marginal in position. The crown, which consists entirely of the vertex, lies at an acute angle with the face and is widest at the centre and posteriorly depressed.

Thorax. The pronotum, which is flattened and laterally wide, is broadest posteriorly and the anterior margin is parallel with the hind margin.

Legs. The fore and middle tibiae are quadrilateral in section and the hind tibiae, which are curved and flattened, have both external edges armed with strong spines.

Tegmina. The tegmina, which are narrow, are blunt apically and have either a wide or a narrow appendix. In forms with a wide appendix the cell enclosed by the arms of Cu_1 , forms part of the overfold of the tegmina. The venation may be normal and complete or else reticulate to a varying degree.

Genitalia. In both sexes the tergites of the ninth segment bear external spines and in the male the sub-genital plates and parameres are long and narrow.

Genera comprised in the Krisnini.

Acostemma Signoret.

1860, *Ann. Soc. ent. Fr.* 8 : 204.

Type—*Acostemma marginalis* Signoret (Madagascar).

Acropona Melichar.

1903, *Homopt. Faun. Ceylon* : 168.

Type—*Gypona prasina* Walker (Ceylon).

Caelidoides Signoret (correction for *Coelidoides* Signoret, 1879).

1880, *Ann. Soc. ent. Fr.* (5) 10 : 205.

Type—*Caelidoides carinatum* Signoret (Madagascar).

Dardania Stål.1866, *Hemipt. Africana* 4 : 113.Type—*Dardania granulosa* Stål (Zanzibar).*Korana* Distant.1910, *Ins. Transvaal* 10 : 241.Type—*Korana maculosa* Distant (South Africa).*Krisna* Kirkaldy (new name for *Siva* Spinola).1900, *Entomologist* 33 : 243.*Siva* Spinola (preoccupied, see *Krisna* Kirkaldy).1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 98, 167.Type—*Siva strigicollis* Spinola (Coromandel).*Taxonomic Notes.*

In 1919, Baker wrote that the Orient possessed an extensive fauna of large jassids related to *Selenocephalus* and that in these insects the antennal scrobes were large and not confined to the cheek, but involved a portion of the lateral surface of the frons, and the lateral margin of the frons thus passed upwards, through the scrobe, and cut the supra-antennal ledges. He divided the jassids with these characteristics into three tribes, the Tartessusaria, the Selenocephalaria and the Stegelytraria, and at the same time he pointed out that some of them possessed a superficial resemblance to Bythoscopids. He also drew attention to the remarkable resemblance between *Krisna*, which he referred to the Stegelytraria, and *Gypona*, but stressed the fact that, in his opinion, this did not denote relationship. Both *Krisna* and *Acropona* were placed by Distant (1908) in the Selenocephalini, and Oshanin (1912) referred *Krisna* and *Stegelytra* to the JASSINAE, Acocephalaria.

I am of the opinion that *Stegelytra* is more closely related to *Coelidia* than to any of the genera listed above, though by no means a typical representative of the COELIDIINAE. The transfer of *Stegelytra*, together with *Iberia*, to the COELIDIINAE, necessitates a new group name, and I have chosen *Krisna* since *Siva*, for which *Krisna* is a new name, is the oldest genus in the tribe.

Gyponini (fig. 30).

Distribution.

Nearctic and Neotropical regions.

Size, Coloration and General Appearance.

The Gyponini range from 5 to 17 mm. in length, and in colour are either green, yellow, or brown, and sometimes they have a bold pattern development.

Food-plants and Habits.

The leaf-hoppers comprised in this tribe have an unusually wide range of food-plants and habitats; thus *Gypona octolineata* Say has been recorded from trees, shrubs, grasses and annuals (Webster, 1913). According to Ball and Reeves (1927) *Ponana scarlatina* Fitch has several varieties, which feed on different plants, some feeding on oak trees and others on herbaceous plants, while *Gypona bipunctulata* Wood feeds exclusively on grasses (Osborn, 1897).

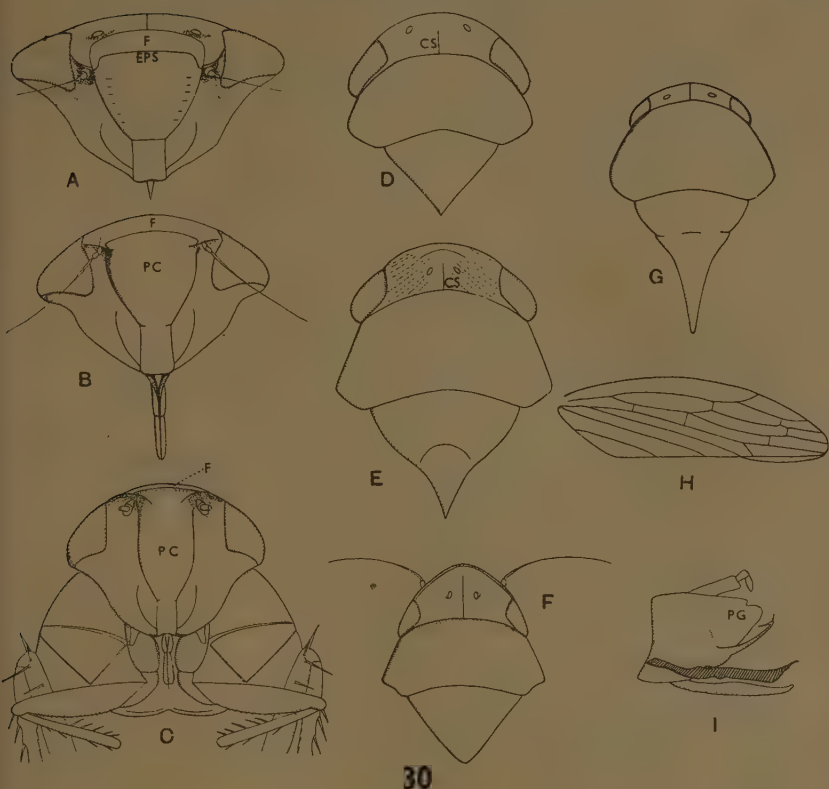


FIG. 30.

A, *Scaris picea* Walk., head ; B, *Polana draba* Ev., head ; C, *Gypona lativitta* Walk., head and part of thorax, in ventral aspect ; D, *Polana draba*, head and thorax, dorsal aspect ; E, *G. lativitta*, head and thorax, dorsal aspect ; F, *Gypona angulata* Spang., head and thorax, dorsal aspect ; G, *Scaris ferruginea* Fabr., head and thorax, dorsal aspect ; H, *Gypona angulata*, tegmen ; I, *G. lativitta*, male genitalia.

Description.

Head. The labium is of moderate length, and the ante-clypeus is sometimes separated from the post-clypeus by a transverse suture. The lora do not reach as far as the margin of the head, and the maxillary plates are wide. The antennal ledges, which are prominent, sharp and curved, and extend on to the post-clypeus, are sometimes oblique, and they may lie close to the hind margin of the face. The epistomal suture may be distinct and arched, and in those species in which the antennae are anteriorly placed, both frontal and post-frontal sutures may be retained. In most forms, all that remains of the frons is a narrow ledge which is compressed between the face and the crown. The crown, which consists entirely of the vertex, is quite distinct from the face and it may either lie at an acute angle with the face, or else its anterior margin may be evenly rounded. The ocelli, which are on the crown, usually lie close to each other on either side of the coronal suture.

Thorax. The pronotum, which is wide laterally and slightly declivous, has the hind margin parallel with, and wider than, the front margin, and it may be laterally produced. The scutellum is large.

Legs. The fore and middle tibiae may either be rounded, or quadrilateral in section. The hind tibiae, which are flattened and curved, have two or three rows of large, strong spines and may have minute spines set between the bases of the largest spines.

Tegmina. The tegmina, which are narrow, have either a wide or a narrow appendix and the venation is of the normal jassid type, or reticulate.

Genitalia. The ninth tergite, in both sexes, bears external spines.

Genera comprised in the Gyponini.

Acusana De Long.

1942, *Ohio State Univ. Mongr.* : 57.

Type—*Acusana veprecula* De Long (North America).

Bulbana De Long.

1942, *Ohio State Univ. Mongr.* : 107.

Type—*Bulbana para* De Long (North America).

Clinonana Osborn.

1938, *Ann. Carnegie Mus.* 27 : 13.

Type—*Clinonana magna* Osborn (French Guiana).

Darma Walker (synonym of *Scaris* Lepeletier and Serville).

1858, *Ins. Saund. Homopt.* : 102.

Type—*Darma bipunctata* Walker (Monte Video).

Dragonana Ball and Reeves.

1927, *Ann. ent. Soc. Amer.* 20 : 489.

Type—*Gypona dracontia* Gibson (Arizona).

Gypona Germar.

1821, *Germ. Mag. Ent.* 4 : 73.

Type—*Cercopis glauca* Fabricius (South America).

Gyponana Ball.

1920, *Ann. ent. Soc. Amer.* 13 : 85.

Type—*Gypona octolineata* Say (North America).

Hamana De Long.

1942, *Ohio State Univ. Mongr.* : 85.

Type—*Gypona dictatoria* Gibson. (Arizona)

Margana De Long.

1942, *Ohio State Univ. Mongr.* : 109.

Type—*Ponana suilla* Ball (Arizona).

Ohausia Schmidt.

1911, *Stett. ent. Zeit.* 72 : 290.

Type—*Ohausia nigra* Schmidt (Ecuador).

Polana De Long.

1942, *Ohio State Univ. Mongr.* : 110.

Type—*Gypona quadrinotata* Spanberg (South Carolina).

Ponana Ball.

1920, *Ann. ent. Soc. Amer.* 13 : 90.

Type—*Ponana scarlatina* Fitch (North America).

Prairiana Ball.

1920, *Ann. ent. Soc. Amer.* 13 : 90.

Type—*Gypona cinerea* Uhler (North America).

Rhogosana Osborn.

1938, *Ann. Carnegie Mus.* 27 : 14.

Type—*Rhogosana rugulosa* Osborn (French Guiana).

Rugosana De Long.1942, *Ohio State Univ. Mongr.* : 64.Type—*Gypona rugosa* Spänberg (Mexico).*Scaris* Lepelletier and Serville.1925, *Encyc. Méthod.* 10 : 609.Type—*Scaris ferruginea* Lepelletier and Serville (South America).*Scaroidana* Osborn.1928, *Ann. Carnegie Mus.* 27 : 49.Type—*Scaroidana flavida* Osborn (Bolivia).*Taxonomic Notes.*

Distant (1907) divided the GYPONINAE into the Penthimiarina and the Hylitaria, and I have already shown in Pt. 2 that the HYLICIDAE are in no way closely related to *Gypona*. Haupt (1929) referred both *Penthimia* and *Bythoscopus* (=JASSUS) to the GYPONINAE, and De Long and Caldwell (1937), as well as placing both *Gypona* and *Penthimia* in this sub-family, also added *Xerophloea*. Oman (1943) has divided the GYPONINAE into two tribes, the Gyponini and the Penthimiini.

Selenocephalini (fig. 31).

Distribution.

All the principal geographical regions, but in Australia limited to North Queensland.

Size, Coloration and General Appearance.

The Selenocephalini range in length from 5 to 10 mm. and in colour they are either some shade of brown (usually reddish-brown), or else they are green. In shape they are either narrow, with tectiform tegmina, or else they are broad and flattened and have widely overlapping tegmina. A few species are brachypterous.

Food-plants and Habits.

Selenocephalus griseus F. has been taken on *Genista* in Europe (Haupt, 1935).

Description.

Head. The face is flattened, the labium short and the ante-clypeus distinct from the post-clypeus. The lora do not reach as far as the anterior margin of the head and the maxillary plates are wide. The post-clypeus encroaches on to the frons to a varying extent and an epistomal suture, as well as frontal and postfrontal sutures, are sometimes retained. The antennae are long, the antennal depressions shallow, and the weak antennal ledges, which are oblique and extend on to the surface of the fronto-clypeus, are nearer to the posterior than to the anterior corners of the eyes. The ocelli are usually situated on a vertical rim, which separates the face from the crown, and they may be either in contact with the eyes or else more centrally placed. The crown is flattened, and in adult insects consists entirely of the vertex, but in the nymphs of some species, which have the head produced, it consists also in part of the frons (fig. 31d). In a few genera (e.g., *Tylissus*) the face and the crown form a continuous curve.

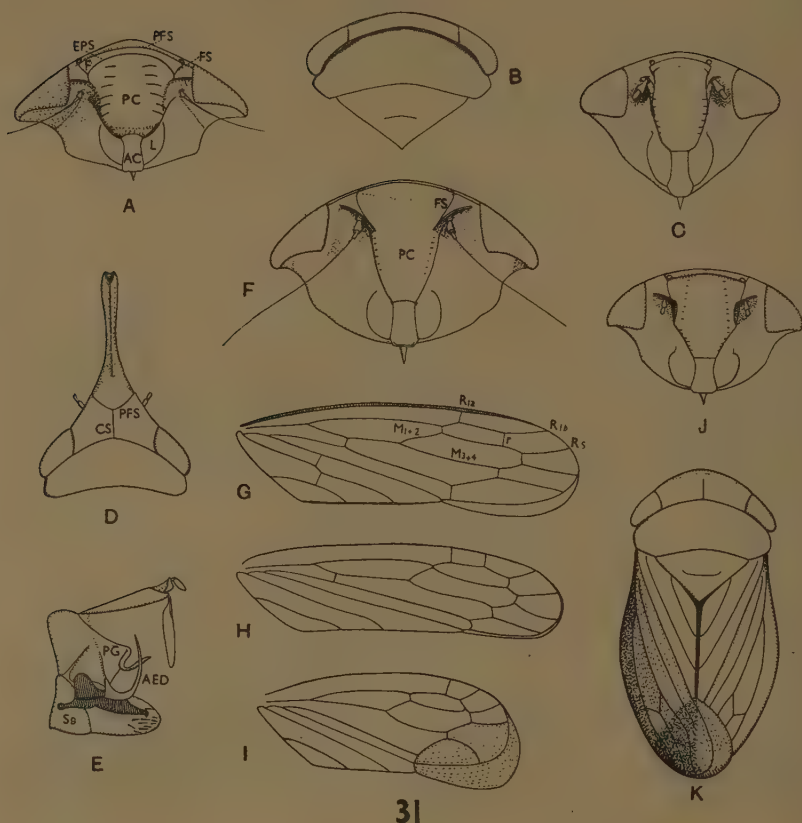


FIG. 31.

A, *Selenocephalus tenebrosa* Dist., head; B, *Kutara grisescens* Ev., head and thorax, dorsal aspect; C, *K. grisescens*, head; D, *Drabescus productus* Ev., head and pronotum of nymph; E, *Selenocephalus africanus* Stål, male genitalia; F, *Drabescus saomana* Osb., head; G, *Drabescus productus*, tegmen; H, *Kutara grisescens*, tegmen; I, *Selenocephalus robustus* Jac., tegmen; J, *Drabescus productus*, head; K, *Selenocephalus tenebrosus* Dist.

Thorax. The pronotum, which is flat, is narrow laterally, but the propleurae separate the eyes from the bases of the tegmina.

Legs. The fore and middle tibiae are rounded, or quadrilateral in section. The hind tibiae are curved and flattened with three rows of long, strong, marginal spines, of which one row may have minute spines set between each large spine.

Tegmina. The tegmina may be either long and narrow, or else short and broad and apically rounded, and the appendix may be wide or narrow. The venation is usually of the normal jassid pattern, but cross-vein $m-cu_2$ is sometimes absent and additional costal veinlets may be present.

Genitalia. The ninth tergite, in both sexes, bears external spines, and in the males the ninth sternite is a separate sclerite.

Genera comprised in the *Selenocephalini*.*Brincadorus* Oman.1936, *Univ. Kansas. Sci. Bull.* 24 : 361.Type—*Brincadorus laticeps* Oman (Brazil).*Carvaka* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 40.Type—*Carvaka picturata* Distant (Southern India).*Cestius* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 309.Type—*Cestius versicolor* Distant (Bengal).*Citorus* Stål.1866, *Hemipt. Africana* 4 : 113.Type—*Selenocephalus decurtatus* Stål (Zanzibar).*Distantia* Signoret.1879, *Ann. Soc. ent. Fr.* 3 : 51, 4 : 65.Type—*Distantia frontalis* Signoret (Port Natal).*Divus* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 365.Type—*Eutettix bipunctatus* Melichar (Ceylon).*Dorada* Melichar.1902, *Berlin ent. Zeit.* 47 : 276.Type—*Dorada lativentris* Melichar (Colombia).*Drabescus* Stål.1870, *Öfvers. Vetens-Akad. Förh. Stockh.* 27 : 738.Type—*Bythoscopus remotus* Walker (Philippines).*Isaca* Walker.1857, *J. Linn. Soc. Lond. (Zool.)* 1 : 172.Type—*Isaca bipars* Walker (Borneo).*Jamitettix* Matsumura.1940, *Ins. Mats.* 15 : 40.Type—*Jamitettix kotonis* Matsumura (Formosa).*Kutara* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 308.Type—*Kutara brunescens* Distant (Ceylon).*Mysolis* Kirkaldy (new name for *Norsia* Walker).1904, *Entomologist* 37 : 279.*Nakula* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 39.Type—*Nakula multicolor* Distant (Burma).*Norsia* Walker (preoccupied, see *Mysolis* Kirkaldy).1869, *J. Linn. Soc. Lond. (Zool.)* 10 : 326.Type—*Norsia flavidorsum* Walker (Mysol).*Norsiana* Distant (new name, invalid, for *Norsia* Walker).1908, *Rec. Ind. Mus.* 2 : 148.*Omanella* Merino.1936, *Philipp. J. Sci.* 61 : 361.Type—*Omanella barberi* Merino (Mindanao).*Parabolopona* Matsumura.1912, *J. coll. Agric. Sapporo* 4 : 288.Type—*Parabolocratus guttatus* Uhler (Japan).*Piezauchenia* Spinola.1852, *Gay. Hist. Fis. y. Pol. de Chile. Zool.* 7 : 287.Type—*Piezauchenia aphropheroides* Spinola (Chile).

Roxasella Merino.

1936, *Philipp. J. Sci.* 61 : 359.

Type—*Roxasella camusi* Merino (Luzon).

Selenocephalus Germar.

1833, *Silb. Rev. Ent.* 1 : 180.

Type—*Jassus obsoletus* Germar (Europe).

Tylissus Stål.

1870, *Öfvers. Vetens.-Akad. Förh. Stockh.* 27 : 739.

Type—*Tylissus nitens* Stål (Philippines).

Taxonomic Notes.

Selenocephalus has been placed in the Acocephalini by Melichar (1903) and Oshanin (1912). Distant (1908) created a separate tribe of the JASSINAE, the Selenocephalaria, and Haupt (1929) and Oman (1943) have recognised this group as a sub-family and tribe of the EUSCELIDAE and the EUSCELINAE respectively.

I have referred *Distantia* to the Selenocephalini since Signoret states that this genus is closely related to *Selenocephalus*, but Signoret's figure illustrating the venation of the tegmen suggests affinity rather with *Platymetopius*.

Jassini¹⁴ (fig. 32).

Distribution.

Universal.

Size, Coloration and General Appearance.

The Jassini range from 3 to 9 mm. in length and in colour they are principally pale green, but they may also be pale brown or pinkish. In appearance they are broad anteriorly and have tectiform tegmina.

Food-plants and Habits.

The majority are arboreal insects, and in Australia several species occur on *Acacia*. In North America *Jassus* (*Bythoscopus*) *distinctus* Van Duzee has been taken on walnut (De Long, 1916) and *J. robustus* Uhler on coarse weeds (Fletcher, 1930). In Europe *J. lanio* L. occurs on oak and *J. microcephala* H.S. on *Helianthemum* (Edwards, 1896).

Description.

Head. The head is evenly convex, and the crown may either be at an acute angle with the face, or form one curved surface with it; sometimes the face is flexed across the antennal axis and there may be no development of a crown at all. The labium is short, or of moderate length, and the ante-clypeus is distinct from the post-clypeus; the lora do not extend as far as the anterior margin of the head and the maxillary plates are wide. There is no trace of an epistomal suture, the fronto-clypeus is circular in outline, and the frontal and postfrontal sutures, if retained, form an even curve. The antennal ledges, which extend on to the fronto-clypeus, are transverse, or slightly oblique and prominent, and they are nearer to the anterior, than to the posterior, corners of the eyes. The antennae are short, or of moderate length, and the antennal depressions are deep. In those species in which the crown is at an acute angle with the face, the ocelli are facial in position, but when a crown is not developed they are vertical and neither on the crown nor yet on the face.

Thorax. The pronotum is wide laterally and slightly declivous.

¹⁴ See footnote on p. 208.

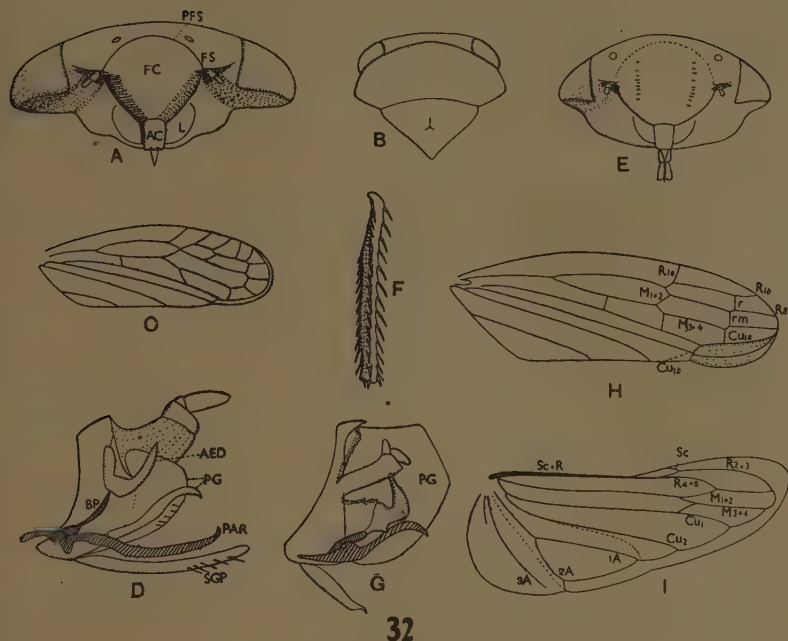


FIG. 32.

A, *Jassus lanio* L., head; B, *J. lanio*, head and thorax, dorsal aspect; C, *J. lanio*, tegmen; D, *Jassus leverii* Ev., male genitalia; E, *Jassus brunomaculatus* Ev., head; F, *J. brunomaculatus*, hind tibia; G, *Jassus compactus* Ev., male genitalia; H, *J. brunomaculatus*, tegmen; I, *J. leverii*, wing.

Legs. The fore and middle tibiae may be either rounded or quadrilateral in section; the hind tibiae are flattened and curved, and two or three rows of marginal spines are long and strong.

Tegmina. The venation of the tegmen is either complete or additional cross-veins may be present. The appendix is of moderate width and sometimes the cubital cell is also involved in the overlap of the tegmina.

Wings. R_{4+5} is fused apically with M_{1+2} .

Genitalia. The ninth tergite, in both sexes, usually bears external spines, and in the male the ninth sternite has lost its separate identity and the sub-genital plates and parameres are usually long and narrow.

Genera comprised in the *Jassini*.

Alloproctus Bergroth.

1923, *Nat. Hist. Juan Fernandez and Easter Is.*, edited by C. Skottsberg 3 : 400.

Type—*Alloproctus amandatus* Bergroth (Juan Fernandez).

Batracomorphus Lewis.

1834, *Trans. ent. Soc. Lond.* 1 : 51.

Type—*Batracomorphus irroratus* Lewis (= *microcephalus* H.S.) (England).

Bythonia Oman.1936, *Univ. Kansas. Sci. Bull.* 24 : 358.Type—*Nionia rugosa* Osborn (Brazil).*Bythoscopus* Germar (synonym of *Jassus* Fabricius, China and Fennah, 1946).1833, *Silb. Rev. Ent.* 1 : 180 (Sept.).Type—*Jassus lanio* Linnaeus (Lewis, 1835) (Europe).*Chinaella* Evans.1936, *Pap. Roy. Soc. Tasm.* 1935 : 76.Type—*Chinaella argentata* Evans (South Australia).*Eurinoscopus* Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 346.Type—*Eurinoscopus lentiginosus* Kirkaldy (Queensland).*Gargaropsis* Fowler (synonym of *Jassus* Fabricius).1896, *Biol. Centr. Amer. Rhyn. Homopt.* 2 : 167.Type—*Gargaropsis innervis* Fowler (Mexico).*Gessius* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 301.Type—*Gessius verticalis* Distant (Burma).*Jassus* Fabricius.1803, *Syst. Rhyn.* : 85.Type—*Jassus lanio* Linnaeus (Europe).*Marquardtella* Schmidt.1930, *Wien. ent. Zeit.* 47 : 122.Type—*Marquardtella krusei* Schmidt (New Guinea).*Ossana* Distant.1913, *Trans. ent. Soc. Lond.* 1913 : 518.Type—*Ossana bicolor* Distant (West Africa).*Pachyopsis* Uhler.1877, *Bull. U.S. Geol. and Geog. Survey* 3 : 466.Type—*Pachyopsis laetus* Uhler (North America).*Pediopsoides* Matsumura (synonym of *Jassus* Fabricius).1912, *J. coll. Agric. Sapporo* 4 : 305.Type—*Pediopsoides formosanus* Matsumura (Formosa).*Prosopoxys* Jacobi.1917, *Voeltzkow Reise in Ostafrika* 3 : 546.Type—*Prosopoxys thoracicus* Jacobi (Madagascar).*Stragania* Stål.1858, *Rio Janeiro Hemipt.* 2 : 49.Type—*Stragania pallescens* Stål (Rio de Janeiro).*Straganiopsis* Baker (synonym of *Pachyopsis* Uhler).1903, *Invert. Pacif.* 1 : 10.Type—*Macropsis idioceroideus* Baker (S.W. North America).*Thalattoscopus* Kirkaldy.1905, *Trans. ent. Soc. Lond.* 1905 : 334.Type—*Thalattoscopus dryas* Kirkaldy (New Britain).*Trocnadella* Pruthi.1930, *Mem. Ind. Mus.* 11 : 9.Type—*Trocnadella shillongensis* Pruthi (Assam).*Taxonomic Notes.*

Until 1929, when Haupt separated *Oncopsis lanio* L. (= *Jassus lanio* L.) from *Macropsis*, *Idiocerus* and *Agallia*, and placed this species, together with *Penthimia*, in the GYPONINAE, all authors had previously

referred these four genera to the BYTHOSCOPIINAE. In 1939b, I presented a new concept of the BYTHOSCOPIDAE, which I have now modified as the result of recent research. *Bythonia* is only tentatively placed in the Jassini.

Trocnadini (fig. 33).

Distribution.

Australia.

Size, Coloration and General Appearance.

Trocnada spp. range from 6 to 9 mm. in length, and in colour are pink, black, brown, or greenish-pink.

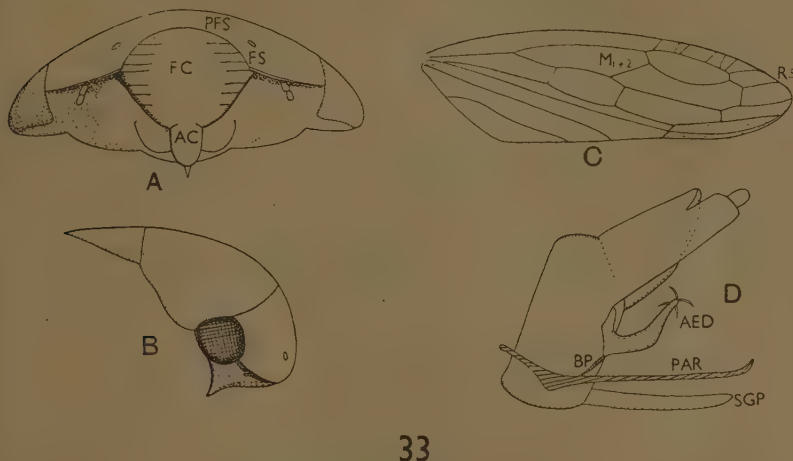


FIG. 33.

A, *Trocnada dorsigera* Walk., head; B, *T. dorsigera*, head and thorax in profile; C, *T. dorsigera*, tegmen; D, *Trocnada minuta* Ev., male genitalia.

Food-plants and Habits.

The Trocnadini are aboreal insects associated exclusively with eucalypts.

Description.

Head. The labium is of moderate length, the lora do not reach as far as the anterior margin of the head and the maxillary plates are wide. No trace remains of a separate frons and the fronto-clypeus is small and approximately circular in outline. The frontal and post-frontal sutures, if retained, form a semi-circle, and the antennal ledges, which are prominent, sharp, wide, transverse and curved, extend on to the fronto-clypeus; the antennae are short and the antennal depressions deep. That part of the face which lies anterior to the antennal ledges is at right-angles to the rest of the head and the latter forms a continuous curve with the pronotum; there is no development of a crown, the coronal suture is lacking and the ocelli are in a vertical position.

Thorax. The pronotum is laterally wide, declivous, and collar-shaped.

Legs. The fore and middle tibiae are quadrilateral in section and somewhat flattened. The hind tibiae are curved and flattened with three rows of strong, prominent marginal spines.

Tegmina. The tegmina, which are long and narrow, have a moderately wide appendix and the cubital cell forms part of the overfold of the tegmina. The venation may be complete but accessory costal veinlets are usually present.

Wings. R_{4+5} is fused apically with M_{1+2} .

Genitalia. The tergite of the ninth segment bears short external spines in both sexes, and in the male the sub-genital plates and parameres are long and narrow, and the ninth sternite does not retain its separate identity.

Genera comprised in the Trocnadini.

Abelterus Stål (synonym of *Trocnada* Walker).

1856, *Öfvers. Vetensk.-Akad. Förh. Stockh.* 22 : 157.

Type—*Abelterus incarnatus* Stål (North Australia).

Trocnada Walker.

1858, *Ins. Saund. Homopt.* : 103.

Type—*Trocnada dorsigera* Walker (New South Wales).

Taxonomic Notes on the Trocnadini.

In 1936 I referred *Trocnada* to the BYTHOSCOPIDAE and later (1939b) confirmed this association. The creation of a separate tribe to contain a single genus, which is clearly very closely related to *Jassus*, has been done in order to draw attention to this genus which furnishes a further example of the divergence of head-shape within the JASSINAE.

Reuterellini¹⁵ (fig. 34).

Distribution.

Australia.

Size, Coloration and General Appearance.

Reuteriella spp. range in length from 7 to 9 mm. and in colour are usually pale green, but may also be green, streaked with dark reddish-brown. In shape they are somewhat flattened and they exhibit marked sexual dimorphism.

Food-plants and Habits.

The Reuteriellini are aboreal insects which feed exclusively on eucalypts.

Description.

Head. The head is considerably flattened, the lora do not reach as far as the anterior margin of the head and the maxillary plates are wide. The post-clypeus is continuous with the frons, and the latter is compressed and flattened, and the postfrontal sutures are obliterated. The antennal ledges, which are sharp, but not prominent, lie close to the posterior corners of the eyes and extend medially on to the fronto-clypeus. The antennae are short, the antennal depressions shallow and the ocelli are situated on a narrow rim which separates the face from the crown. The crown is flattened and widely produced.

Thorax. The pronotum, which is dorsally flat and laterally wide, is wider posteriorly than anteriorly.

Legs. The fore and middle tibiae are rounded and the hind tibiae are curved and flattened with three rows of strong, prominent marginal spines.

¹⁵ For further illustrations, see Evans, 1939a, b ; 1941.

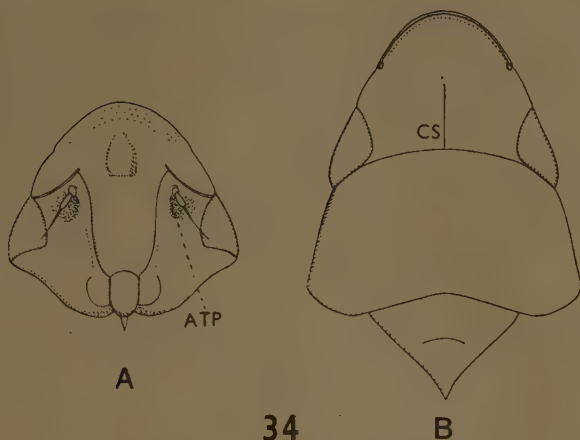


FIG. 34.—*Reuteriella flavescens* Sign.
A, head ; B, head and thorax, dorsal aspect.

Tegmina. The tegmina, which are long and narrow, have complete venation and a wide appendix, and the cubital cell forms part of the overfold of the tegmina.

Wings. R_{4+5} is fused apically with M_{1+2} .

Genitalia. The tergite of the ninth segment usually bears external spines in both sexes, and in the male the parameres are long and narrow and the ninth sternite does not retain its separate identity.

Genera comprised in the Reuterellini.

Reuteria Signoret (see *Reuteriella* Signoret).

1880, *Ann. Soc. ent. Fr.* (5) 10 : 45.

Type—*Reuteria flavescens* Signoret (Tasmania).

Reuteriella Signoret (new name for *Reuteria* Signoret).

1880, *Ann. Soc. ent. Fr.* (5) 10 : 365.

Taxonomic Notes.

In 1939a, I referred *Reuteriella* to the EUSCELIDAE and associated it with *Hecalus*, but later (1939b) on realising that, in spite of the fact that species in this genus had flattened heads and marginal ocelli, they were clearly derivatives of *Jassus* (*Bythoscopus*), I transferred the genus, together with *Hecalus*, to the BYTHOSCOPIIDAE; and in 1941 I referred also *Spanbergiella* and *Parabolocratus* to the BYTHOSCOPIIDAE. Further study has made it clear that I was in error with regard to the placing of *Hecalus*, *Spanbergiella* and *Parabolocratus*.

Discussion of the JASSINAE (BYTHOSCOPINAE).

The extreme plasticity of the head in this sub-family has tended in the past to obscure the true inter-relationships of the several comprised groups. I suggest that the group of genera comprised in the JASSINAE has been derived from a jassid with a head somewhat of the type illustrated in fig. 28a.

If fig. 31*a* is compared with figs. 28*a*, 29*a* and 30*a*, the close similarity existing between the various types of jassine heads will be evident. From such types of head the typical gyponid head (fig. 30*c*) has been achieved by the backward development of the post-clypeus accompanied by the movement of the antennae and the antennal ledges, which have come to lie against the hind margin of the face. This backward movement has resulted in the frons becoming compressed and marginal in position; the accompanying flattening and anterior production of the crown has involved a change in the position of the ocelli, which instead of being situated close to the apices of the frontal sutures, have come to lie close to each other on either side of, and posterior to, the apex of the coronal suture.

In the Selenocephalini, the frons, while remaining entirely on the face of the head, has become amalgamated with the post-clypeus, and the ocelli have remained on the rim-like anterior margin of the crown.

The Penthimiini might well be divided into several sub-tribes, but it is doubtful whether these would include genera with such distinct characters as not to involve overlapping.

The Jassini, Trocnadini and the Reuteriellini form a group distinct from the remainder of the JASSINAE, since not only do they lack any trace of a separate frons, but in every species comprised in these three tribes the venation of the wings is reduced in an identical manner.

Quite apart from these similarities of a structural nature there is a marked resemblance in general shape, appearance, and coloration between the representatives of the various tribes and this is especially noticeable between certain of the Penthimiini and the Selenocephalini and also between the Krisnini and the Gyponini.

EUSCELINAE.

The EUSCELINAE comprise a large group of genera which may well have been derived from a jassine stem. I propose to divide them into five tribes, the Euscelini, Platymetopiini, Xestocephalini, Balcluthini and Macrostelini, but at the same time acknowledge that other well-defined natural groups may exist within this sub-family which I have failed to recognise.

Euscelini (fig. 35*a-f, j, k*; 36*a-c*).

Distribution.

Universal, but especially well represented in the Palaearctic, Nearctic and Neotropical regions.

Size, Coloration and General Appearance.

The Euscelini range in length from 3 to 11 mm. and in colour may be brown, grey, green or black; they are mostly of a drab appearance, but a few have a striking colour pattern and several are brachypterous.

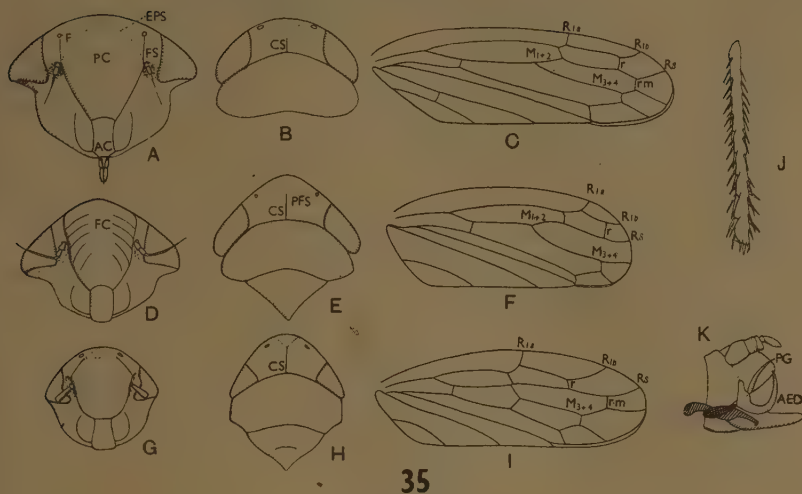


FIG. 35.

A, *Remadosus magnus* Osb. and Ball, head; B, *Eutettix slosoni* Van Duzee, head and pronotum, dorsal aspect; C, *Remadosus magnus*, tegmen; D, *Euscelis lineolata* Brulle, head; E, *E. lineolata*, head and thorax, dorsal aspect; F, *E. lineolata*, tegmen; G, *Xestocephalus pulicarius* Van Duzee, head; H, *X. pulicarius*, head and thorax, dorsal aspect; I, *X. pulicarius*, tegmen; J, *Norvellina seminuda* Say, hind tibia; K, *N. seminuda*, male genitalia.

Food-plants and Habits.

While these insects are associated especially with grasses, several have other food-plants. Thus *Opsiurus stactogalus* Fieber feeds on Tamarisk (Harding, 1930) and species in the genera *Colladonus*, *Conodonus* and *Idiodonus* are tree- and shrub-inhabiting forms (Ball, 1936). According also to Ball (1932) there are no grass-feeders in the genera *Aligia*, *Mesamia*, *Phlepsius* and *Eutettix*, and several species of *Exitianus*, which are general grass-feeders, breed only on a single grass. Helson (1942) has investigated the bionomics of *Orosius* (*Thamnotettix*) *argentata* Evans, a species well known as a virus transmitter in Australia.

Description.

Head. The face of the head is wide, slightly convex, and somewhat emarginate beneath the eyes, and the face and the crown usually form a single curved surface. The labium is short, or of moderate length, and the maxillary plates are wide. The antennae, which are usually nearer to the anterior than to the posterior corners of the eyes, are of variable length, the antennal ledges are either reduced or absent and the antennal depressions shallow. Although vestiges of a reduced, but distinct, ventral frons may be retained, this is an unusual feature, but frontal sutures are invariably present and parallel to the inner margins of the eyes. Postfrontal sutures are seldom in evidence, and when present are vestigial and lie close to the hind margin of the face, except in those forms where the head is produced, when they may become dorsal in position. The ocelli are marginal and lie close to the apices of the frontal sutures, and the crown, which is seldom sharply separated from the face, is usually of equal width with the eyes and but seldom produced.

Thorax. The pronotum is usually, but not invariably, narrow laterally.

Legs. The hind tibiae are somewhat flattened and have two or three rows of long, strong, marginal spines.

Tegmina. The tegmina, which have complete venation, are usually rounded apically and frequently they are reduced to a varying degree. In many forms R_{1a} and R_{1b} are widely spaced and at right-angles to the costal border.

Genera comprised in the Euscelini.

Acinopterus Van Duzee.

1892, *Psyche* 6 : 307.

Type—*Acinopterus acuminatus* Van Duzee (North America).

Aconura Lethierry.

1876, *C. R. Ann. Soc. ent. Belg.* 19 : 85.

Type—*Aconura jakowleffi* Lethierry (Astrakan).

Adoratura (Kuznetzov) Lindberg and Zachvatkin.

1936, *Arkiv. für Zool. Svensk Vetensk.* 29a : 13.

Type—*Doratura heros* Melichar (Persia).

Alaca Oman.

1936, *Univ. Kansas. Sci. Bull.* 24 : 386.

Type—*Alaca longicauda* Oman (Argentina).

Alapus De Long and Sleesman.

1929, *Ann. ent. Soc. Amer.* 22 : 86.

Type—*Deltocephalus fraternus* Ball (North America).

Aligia Ball.

1907, *Proc. Iowa Acad. Sci.* 12 : 31, 53.

Type—*Jassus jucunda* Uhler (Western North America).

Alituralis Merino (new name, invalid, for *Aliturus* Distant).

1937, *Philipp. J. Sci.* 61 : 388.

Aliturus Distant (preoccupied, see *Neoaliturus* Distant).

1908, *Faun. Brit. Ind. Rhyn.* 4 : 398.

Type—*Aliturus gardineri* Distant (Laccadive Islands).

Allectus Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 75.

Type—*Allectus notatus* Distant (India).

Allophleps Bergroth.

1920, *Arkiv. für Zool. Stockholm* 12 : 27.

Type—*Allophleps inspersa* Bergroth (East Africa).

Allygianus Ball.

1936, *Bull. Brooklyn ent. Soc.* 31 : 59.

1936, *J. Wash. Acad. Sci.* 26 : 431.

Type—*Thamnotettix gutturosa* Ball (North America).

Allygus (Fieber) Scott.

1875, *Rev. Mag. Zool.* 1875 : 410, 1876 : t. 13.

1876, *Ent. mon. Mag.* 12 : 169 (Jan.).

Type—*Jassus mixtus* Fabricius (France).

Amblysellus Sleesman.

1930, *Ent. Amer.* 10 : 131.

Type—*Athysanus curtisii* Fitch (North America).

Amphipyga Osborn.

1928, *Ohio biol. Survey Bull.* 14 : 289.

1930, *Ann. ent. Soc. Amer.* 23 : 691.

Type—*Amphipyga balli* Osborn (Ohio).

- Amplicephalus* De Long.
1926, *Ohio State Univ. Studies* 2, no. 13 : 20, 83.
Type—*Deltiocephalus osborni* Van Duzee (North America).
- Anemochrea* Kirkaldy.
1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 329.
Type—*Anemochrea mitis* Kirkaldy (New South Wales).
- Anemolua* Kirkaldy.
1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 329.
Type—*Anemolua hanuala* Kirkaldy (Queensland).
- Anoplotettix* Ribaut.
1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 4.
Type—*Thamnotettix fuscovenosus* Ferrari (Europe).
- Artianus* Ribaut.
1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 7.
Type—*Jassus interstitialis* Germar (Europe).
- Artucephalus* De Long.
1944, *Ann. ent. Soc. Amer.* 36 : 654.
Type—*Artucephalus fasciatus* De Long (Mexico).
- Arundanus* De Long.
1935, *Ent. News.* 46 : 180.
Type—*Arundanus arundineus* De Long (Tennessee).
- Arya* Distant.
1908, *Faun. Brit. Ind. Rhyn.* 4 : 338.
Type—*Arya rubrolineata* Distant (Bengal).
- Ascius* De Long.
1943, *Ohio J. Sci.* 43 : 251.
Type—*Ascius triangularis* De Long (Mexico).
- Atanus* Oman.
1936, *Univ. Kansas Sci. Bull.* 24 : 381.
Type—*Eutettix dentatus* Osborn (Bolivia).
- Athysanella* Baker (synonym of *Aconura* Leth.).
1898, *Psyche* 8 : 185.
Type—*Athysanella magdalena* Baker (New Mexico).
- Athysanopsis* Matsumura.
1905, *Thousand Ins. Japan* 2 : 65.
1914, *J. Coll. Agric. Sapporo* 5 : 184.
Type—*Athysanopsis salicis* Matsumura (Japan).
- Athysanus* Burmeister.
1838, *Gen. Ins.* 1 : 14.
Type—*Cicada argentatus* Fabricius (France).
- Bahita* Oman.
1936, *Univ. Kansas Sci. Bull.* 24 : 379.
Type—*Eutettix infuscatus* Osborn (Brazil).
- Ballana* De Long.
1936, *Ohio J. Sci.* 36 : 217.
Type—*Thamnotettix vetula* Ball (Western North America).
- Bandara* Ball.
1931, *Bull. Brooklyn ent. Soc.* 26 : 93.
Type—*Eutettix johnsoni* Van Duzee (North America).
- Banus* Distant.
1908, *Faun. Brit. Ind. Rhyn.* 4 : 353.
Type—*Banus oblatatus* Distant (Ceylon).

Baroma Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 378.Type—*Baroma reticulata* Oman (Argentine).*Benala* Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 390.Type—*Deltocephalus tumidus* Osborn (Bolivia).*Bhatia* Distant.1908, *Faun. Brit. Ind. Rhyn.* **4** : 357.Type—*Bhatia divacea* Melichar (Ceylon).*Bilusius* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* **77** : 2.Type—*Anoterostemma noualhieri* Melichar (Europe).*Bolarga* Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 366.Type—*Parablocratus bolivianus* Osborn (Bolivia).*Bothrognathus* Berg (new name, invalid, for *Aliturus* Distant).1920, *Ark. Zool.* **12** : 29.*Brazoza* Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 386.Type—*Thamnotettix picturellus* Baker (Brazil).*Calana* De Long (preoccupied, see *Calanana* De Long).1936, *Ohio J. Sci.* **36** : 218.Type—*Thamnotettix umbricatus* Ball (North America).*Calanana* De Long (new name for *Calana* De Long).1944, *Ohio J. Sci.* **44** : 272.*Calliscarta* Stål.1869, *Köngl. Svensk. Vet.-Ak. Handl.* **8** : 82.Type—*Cicada decora* Fabricius (South America).*Cariancha* Oman.1936, *Univ. Kansas Sci. Bull.* **24** : 360.Type—*Cariancha caribola* Oman (Brazil).*Cechenotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* **77** : 4.Type—*Thamnotettix martini* Lethierry (Europe).*Cenedaeus* Distant.1908, *Faun. Brit. Ind. Rhyn.* **4** : 296.Type—*Cenedaeus horvarthi* Distant (Bombay).*Chlorotettix* Van Duzee.1892, *Psyche* **6** : 306.Type—*Bythoscopus unicolor* Fitch (North America).*Cicadula* Zetterstedt.1838, *Ins. Lapp.* : 295.Type—*Cicada quadrinotata* Fabricius (France).*Cicaduloidea* Osborn.1935, *Bull. Bishop. Mus.* **114** : 258.Type—*Cicaduloidea pacifica* Osborn (Marquesas Islands).*Circulifer* Zachvatkin.1935, *Wiss. Ber. Moskauer Staats Univ.* **4** : 111.Type—*Thamnotettix unicolor* Haupt (Europe).*Colladonus* Ball.1936, *Bull. Brooklyn ent. Soc.* **31** : 57.Type—*Thamnotettix collaris* Ball (North America).

Commellus Osborn and Ball.1902, *Ohio Nat.* 11 : 232.Type—*Athysanus comma* Van Duzee (North America).*Conala* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 396.Type—*Spanbergiella fasciata* Osborn (Brazil).*Conodonus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 58.Type—*Thamnotettix flavocapitatus* Van Duzee (North America).*Conosanus* Osborn and Ball (synonym of *Euscelis* Brulle).1902, *Ohio Nat.* 2 : 231, 236.Type—*Athysanus obsoletus* Kirschbaum (Germany).*Cortona* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 390.Type—*Cortona minuta* Oman (Argentina).*Coryphaeus* Puton (invalid emendation of *Coryphaeus* Fieber).1886, *Cat. Hemipt.* : 81.*Coryphaeus* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 503.Type—*Jassus gyllenhali* Fallen (Sweden).*Cosmotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 9.Type—*Jassus caudatus* Flor (Europe).*Cumora* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 374.Type—*Cumora angulata* Oman (Argentina).*Cyperana* De Long.1936, *Ohio J. Sci.* 36 : 218.Type—*Thamnotettix melanogaster* Provancher (Eastern North America).*Dagama* Distant.1910, *Ins. Transvaal* 10 : 243.Type—*Dagama novata* Distant (Natal).*Deltocephalus* Burmeister.1838, *Gen. Ins.* 1 : pl. 14, sub-gen. 3.Type—*Cicada abdominalis* Fallen (Fieber, 1866) (Palearctic).*Deltorynchus* De Long.1943, *Ohio J. Sci.* 43 : 79.Type—*Deltorynchus spinosus* De Long (Mexico).*Dio* Distant (synonym of *Deltocephalus* Burmeister).1918, *Faun. Brit. Ind. Rhyn.* 7 : 56.Type—*Dio facialis* Distant (Himalayas).*Distomotettix* Ribaut.1938, *Bull. Soc. Hist. nat. Toulouse* 72 : 97.Type—*Jassus fenestratus* Herrich-Schaffer (Europe).*Divitiacus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 5.Type—*Divitiacus primus* Distant (India).*Dixianus* Ball.1918, *Ann. ent. Soc. Amer.* 11 : 387.Type—*Dixianus utahns* Ball (S.W. North America).*Dochmocar* Thomson (synonym of *Paramesus* Fieber).1869, *Opusc. Ent.* 1 : 65.Type—*Cicada nervosus* Fallen (Sweden).

Doleranus Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 58.Type—*Thamnotettix longula* Gillette and Baker (North America).*Doliotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 8.Type—*Cicada pallens* Zetterstedt (Europe).*Doratulina* Melichar.1903, *Homopt. Faun. Ceylon* : 198.Type—*Doratulina jocosus* Melichar (Ceylon).*Doraturopsis* Lindberg (synonym of *Adoratura* Lindberg and Zachvatkin).1935, *Wiss. Ergeb. Niederl. Exped. Karakorum, Leipzig, Hemipt.* : 423.Type—*Doraturopsis acutus* Lindberg (= *Doratura heros* Melichar) (Central Asia).*Driotura* Osborn and Ball.1898, *Proc. Davenport Acad. Sci.* 7 : 87.Type—*Athysanus gammaroides* Van Duzee (North America).*Drylix* Edwards (synonym of *Cicadula* Zetterstedt).1922, *Ent. mon. Mag.* 58 : 206.Type—*Cicada striola* Fallen (Europe).*Duranturopsis* Melichar.1908, *Casopis Ceske Spolec. Entom.* 5 : 13.Type—*Duranturopsis katonae* Melichar (East Africa).*Ederranus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 9.Type—*Athysanus discolor* J. Sahlberg (Europe).*Edwardsiastes* Kirkaldy (new name for *Glyptocephalus* Edwards, a synonym of *Rhytistylus* Fieber.).1900, *Entomologist* 33 : 243.*Elymana* De Long.1936, *Ohio J. Sci.* 36 : 218.Type—*Thamnotettix inornatus* Van Duzee (North America).*Epitettix* Matsumura.1914, *J. Coll. Agric. Sapporo* 5 : 194.Type—*Epitettix hiroglyphicus* Matsumura (Formosa).*Eremophlepsius* Zachvatkin.1924, *Ent. Mitt.* 13 : 127.Type—*Eremophlepsius rohdendorfi* Zachvatkin (Transcaspia).*Euleimonios* Kirkaldy (synonym of *Cicadula* Zetterstedt).1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 342.Type—*Euleimonios dimittendus* Kirkaldy (New South Wales).*Euscelidius* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 10.Type—*Jassus variegatus* Kirschbaum (Europe).*Euscelis* Brullé.1882, *Exped. scient. de Voy. en Morée* 3, Ins. pt. 1 : 90, 109.Type—*Euscelis lineolatus* Brullé (North Africa).*Eusceloidea* Osborn.1923, *Ann. Carnegie Mus.* 15 : 46.Type—*Eusceloidea nitida* Osborn (Bolivia).*Eusceloscopus* Evans.1943, *Trans. Roy. Soc. W. Aust.* 27 : 147.Type—*Eusceloscopus yanchepensis* Evans (Western Australia).

Eutettix Van Duzee.1892, *Psyche* 6 : 307.Type—*Thamnotettix luridus* Van Duzee (North America).*Exitianus* Ball.1929, *Trans. Amer. ent. Soc.* 55 : 5.Type—*Cicadula exitiosa* Uhler (North America).*Faltala* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 385.Type—*Faltala brachyptera* Oman (Northern Argentina).*Fieberia* Signoret (see *Fieberiella* Signoret).1879, *Ann. Soc. ent. Fr.* (5) 9 : 52.Type—*Selenocephalus flori* Stål (Greece).*Fieberiella* Signoret (new name for *Fieberia* Signoret).1880, *Ann. Soc. ent. Fr.* (5) 10 : 67, 365.*Flexamia* De Long.1926, *Ohio state Univ. Studies* 2, no. 13 : 20, 22.Type—*Deltocephalus reflexus* Osborn and Ball (North America).*Friscananus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 60.Type—*Thamnotettix intricatus* Ball (North America).*Galerius* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 78.Type—*Galerius indicatrix* Distant (South India).*Gillettiella* Osborn.1930, *Ann. ent. Soc. Amer.* 23 : 689.Type—*Aconura labiata* Gillette (Colorado).*Gladionura* Osborn.1930, *Ann. ent. Soc. Amer.* 23 : 706.Type—*Aconura argenteola* Uhler (Colorado).*Gloridonus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 58.Type—*Thamnotettix gloriosus* Ball (North America).*Glyptocephalus* Edwards (preoccupied, see *Edwardsiastes* Kirkaldy).1883, *Ent. mon. Mag.* 1883 : 148.Type—*Athysanus canescens* Douglas and Scott (England).*Goniagnathus* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 506.Type—*Jassus brevis* Herrich-Schaeffer (Germany).*Goniozygum* Bergroth (new name, invalid, for *Goniagnathus* Fieber).1920, *Ark. Zool.* 12 : 29.*Graminella* De Long.1936, *Ohio J. Sci.* 36 : 218.Type—*Thamnotettix aureovittatus* Sanders and De Long (North America).*Graphocraerus* Thomson.1869, *Opusc. Ent.* 1 : 57.Type—*Cicada ventralis* Fallen (Sweden).*Grypotes* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 17 : 503.Type—*Jassus puncticolis* Herrich-Schaeffer (Germany).*Gunghuyana* Distant.1910, *Ins. Transvaal.* 10 : 244.Type—*Gunghuyana gazana* Distant (South Africa).

Handianus Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 7.Type—*Jassus procerus* Herrich-Schaeffer (Europe).*Hardya* Edwards.1922, *Ent. mon. Mag.* 58 : 206.Type—*Aphrodes melanopsis* Hardy (England).*Hebecephalus* De Long.1926, *Ohio State Univ. Studies* 2, no. 13 : 20, 58.Type—*Deltocephalus signatifrons* Van Duzee (North America).*Hecaloidea* Osborn.1923, *Ann. Carnegie Mus.* 15 : 28.Type—*Hecaloidea nervosa* Osborn (Bolivia).*Hegira* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 383.Type—*Hegira brunnea* Oman (Argentina)*Henschia* Lethierry.1892, *Rev. Ent.* 11 : 69.Type—*Henschia seticauda* Lethierry (Hungary).*Hesium* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 4.Type—*Cicada biguttata* Fallen (Europe).*Hyposadianus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 6.Type—*Thamnotettix torneellus* Zetterstedt (Europe).*Idiodonus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 57.Type—*Thamnotettix kennicotti* Uhler (North America).*Iowanus* Ball.1918, *Ann. ent. Soc. Amer.* 11 : 382.Type—*Iowanus handlirschi* Ball (Central America).*Jassargus* Zachvatkin.1934, *Mem. Soc. ent. Ital.* 12 : 268.Type—*Deltocephalus bisubulatus* Then (Tyrol).*Kinonia* Ball.1933, *Bull. Brooklyn ent. Soc.* 28 : 224.Type—*Kinonia elongata* Ball (North America).*Kirkaldiella* Osborn.1935, *Bull. Bishop Mus.* 134 : 13.Type—*Kirkaldiella euphorbiae* Osborn (Hawaii).*Knullana* De Long.1941, *Ohio. J. Sci.* 41 : 86.Type—*Thamnotettix perezigua* Ball (North America).*Laburrus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 9.Type—*Athysanus limbatus* Ferrari (Europe).*Laevicephalus* De Long (synonym of *Deltocephalus* Burmeister).1926, *Ohio. State Univ. Studies* 2, no. 13 : 21, 64.Type—*Deltocephalus sylvestris* Osborn and Ball (North America).*Lampridius* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 58.Type—*Lampridius spectabilis* Distant (Burma).*Lamprotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 9.Type—*Cicada octopunctata* Schrank (Europe).

Latalus De Long and Sleesman.1929, *Ann. ent. Soc. Amer.* 22 : 87.Type—*Amblycephalus sayi* Fitch (North America).*Limotettix* J. Sahlberg (synonym of *Cicadula* Zetterstedt).1871, *Not. Sällsk. Faun. Flor. Fennica* 9 : 224.Type—*Cicada striola* Fallen (Europe).*Lonatura* Osborn and Ball.1898, *Proc. Davenport Acad. Sci.* 8 : 83.Type—*Lonatura catalina* Osborn and Ball (North America).*Macustus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 3.Type—*Cicada grisea* Zetterstedt (Europe).*Maximianus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 79.Type—*Maximianus notatus* Distant (South India).*Megabyzus* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 294.Type—*Megabyzus signandus* Distant (Ceylon).*Melichariella* Matsumura (preoccupied, synonym of *Bhatia* Distant).1914, *J. Coll. Agric. Sapporo* 5 : 236.Type—*Melichariella satsumensis* Matsumura (Japan).*Menosoma* Ball.1931, *Florida Ent.* 15 : 5.Type—*Menosoma stonei* Ball (North America).*Mesotettix* Matsumura.1914, *J. Coll. Agric. Sapporo* 5 : 195.Type—*Mesotettix shokaensis* Matsumura (Formosa).*Metathysanus* Dahl (synonym of *Euscelis* Brullé).1912, *Beitr. Naturdenk. malpfl.* 3 : 439.Type—*Athysanus obsoletus* Kirschbaum (Germany).*Mexicananus* De Long.1944, *Ohio J. Sci.* 44 : 89.Type—*Mexicananus levis* De Long (Mexico).*Mimodrylix* Zachvatkin (synonym of *Exitianus* Ball).1935, *Wiss. Ber. Moskauer Staats. Univ.* 4 : 108.Type—*Athysanus capicola* Stål (South Africa).*Mimotettix* Matsumura.1914, *J. Coll. Agric. Sapporo* 5 : 197.Type—*Mimotettix kawamurae* Matsumura (Formosa).*Mocydia* Edwards.1922, *Ent. mon. Mag.* 58 : 206.Type—*Jassus croceus* Herrich-Schaeffer (Germany).*Mocydiopsis* Ribaut.1939, *Bull. Soc. Hist. nat. Toulouse* 73 : 8.Type—*Jassus attenuatus* Germar (Europe).*Monobazus* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 351.Type—*Monobazus himalayensis* Distant (North India).*Myittana* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 340.Type—*Myittana dohertyi* Distant (Tenasserim).*Neoliturus* Distant (new name for *Aliturus* Distant).1918, *Faun. Brit. Ind. Rhyn.* 7 : 63.

Neobala Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 396.Type—*Thamnotettix pallidus* Osborn (South America).*Nephoris* Jacobi.1912, *Ergebn. Deutsch. Zentr. Afrik. Exp.* 4 : 39.Type—*Nephoris chalybaea* Jacobi (Central Africa).*Nephrotettix* Matsumura.1902, *Termez. Füzet.* 25 : 356, 378.Type—*Selenocephalus cincticeps* Uhler (= *apicalis* Motsch.) (Japan).*Nesaloha* Oman (synonym of *Orosius* Distant).1943, *Pan-Pacific Ent.* 19 : 33.Type—*Nesaloha cantonensis* Oman (Canton Is.).*Nesophrosyne* Kirkaldy.1907, *Proc. Hawaiian Ent. Soc.* 1 : 160.Type—*Eutettix perkinsi* Kirkaldy (Hawaii).*Nesophryne* Kirkaldy.1907, *Proc. Hawaiian ent. Soc.* 1 : 160.Type—*Nesophryne filicola* Kirkaldy (Hawaii).*Nesoreias* Kirkaldy.1910, *Fauna Hawaii* 2 : 573.Type—*Nesoreias insularis* Kirkaldy (Hawaii).*Nesoriella* Osborn.1935, *Bull. Bishop Mus.* 134 : 248.Type—*Nesoriella maculata* Osborn (Marquesas Islands).*Neurotettix* Matsumura.1914, *J. Coll. Agric. Sapporo.* 5 : 192.Type—*Neurotettix horishanus* Matsumura (Formosa).*Norvellina* Ball.1931, *Canad. Ent.* 63 : 3.Type—*Eutettix mildredae* Ball (North America).*Occiplanocephalus* Evans.1943, *Trans. Roy. Soc. W. Aust.* 27 : 146.Type—*Occiplanocephalus rarus* Evans (Western Australia).*Ollarianus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 59.Type—*Eutettix balli* Van Duzee (Arizona).*Omanana* De Long.1941, *Lloydia* 4 : 293.Type—*Athysanus litigiosa* Ball (Mexico).*Onura* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 387.Type—*Onura eburneola* Oman (Argentina).*Ophiola* Edwards.1922, *Ent. mon. Mag.* 58 : 206.Type—*Cicada striatula* Fallen (Sweden).*Opsius* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 505.Type—*Jassus* (*Thamnotettix*) *tamaricis* Kirschbaum (Germany).*Orientus* De Long.1938, *Ohio J. Sci.* 38 : 217.Type—*Phlepsius ushidae* Matsumura (Japan).*Crobia* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 9.Type—*Cicada cruentata* Panzer (Europe).

Orosius Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 85.Type—*Orosius albicinctus* Distant (South India).*Oxytettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 5.Type—*Jassus viridinervis* Kirschbaum (Europe).*Paivanana* Distant (synonym of *Aconura* Lethierry).1918, *Faun. Brit. Ind. Rhyn.* 7 : 95.Type—*Paivanana indra* Distant (Bengal).*Paluda* De Long.1937, *Amer. Middl. Nat.* 18 : 233.Type—*Thamnotettix placidus* Osborn (= *mellus* Sanders and De Long) (North America).*Palus* De Long and Slesman.1929, *Ann. ent. Soc. Amer.* 22 : 85.Type—*Deltocephalus delector* Sanders and De Long (North America).*Paralimnus* Matsumura.1902, *Termez. Füzet.* 15 : 356, 386.Type—*Paralimnus fallaciosus* Matsumura (Japan).*Parallogyus* Melichar.1903, *Homopt. Faun. Ceylon* : 179.Type—*Parallogyus divaricatus* Melichar (Ceylon).*Paramesus* Fieber.1866, *Verh. zool.-bot. Ges.* 20 : 506.Type—*Athysanus obtusifrons* Stål (= *Cicada nervosus* Stål) (Sweden).*Paraphlepsius* Baker.1897, *Canad. Ent.* 29 : 158.Type—*Paraphlepsius ramosus* Baker (New York).*Pasadenus* Ball.1936, *Bull. Brooklyn ent. Soc.* 31 : 60.Type—*Thamnotettix pasadenus* Ball (North America).*Pectinapyga* Osborn.1930, *Ann. ent. Soc. Amer.* 23 : 697.Type—*Pectinapyga texana* Osborn (Texas).*Pendarus* Ball.1927, *Canad. Ent.* 59 : 262.Type—*Phlepsius slossoni* Ball (North America).*Penestirellus* Beamer and Tuthill.1934, *J. Kansas ent. Soc.* 7 : 22.Type—*Phlepsius catalinus* Beamer and Tuthill (Arizona).*Perotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 2.Type—*Thamnotettix pictus* Lethierry (Europe).*Phlepsius* Fieber.1866, *Verh. zool.-bot. Ges. Wien.* 16 : 503.Type—*Phlepsius maculatus* Fieber (= *Jassus intricatus* H.S.) (Europe).*Phlogotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 4.Type—*Jassus cyclops* Mulsant and Rey (Europe).*Phrynomorphus* Curtis (synonym of *Euscelis* Brullé).1833, *Ent. Mag.* 1 : 194 (Jan.).Type—*Phrynomorphus nitidus* Curtis (= *lineolatus* Brullé) (Britain).

Phrynophyes Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 327.Type—*Phrynophyes phrynophyes* Kirkaldy (Queensland).*Phycotettix* Haupt.1929, *Zool. Jb.* 58 : 260.Type—*Thamnotettix paryphantus* Lethierry (Spain).*Pithyotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 3.Type—*Cicada abietina* Fallen (Europe).*Placotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* 77 : 4.Type—*Thamnotettix taeniatifrons* Kirschbaum (Europe).*Polyamia* De Long.1926, *Ohio State Univ. Studies* 2, no. 13 : 20, 46.Type—*Deltocephalus weedi* Van Duzee (North America).*Prasutagus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 53.Type—*Prasutagus pulchellus* Distant (South India).*Premanus* De Long.1944, *Pan-Pacific Ent.* 20 : 98.Type—*Premanus hebatus* De Long (Mexico).*Protaenia* Thomson (synonym of *Grypotes* Fieber).1869, *Opusc. Ent.* 1 : 58.Type—*Jassus pineleleus* Zetterstedt (Sweden).*Psamotettix* Haupt.1929, *Zool. Jb.* 58 : 262.Type—*Thamnotettix maritimus* Perris (France).*Pseudophlepsius* Zachvatkin.1944, *Ent. Mitt.* 13 : 128.Type—*Phlepsius binotatus* (Fieber) Signoret (South Russia).*Pygotettix* Matsumura.1940, *Ins. Mats.* 15 : 41.Type—*Pygotettix formosanus* Matsumura (Formosa).*Recilia* Edwards.1922, *Ent. mon. Mag.* 58 : 206.Type—*Jassus coronifer* Marsh (Europe).*Remadosus* Ball.1929, *Trans. Amer. ent. Soc.* 55 : 3.Type—*Athyasus magnus* Osborn and Ball (North America).*Retusanus* De Long.1945, *Pan-Pacific Ent.*, 21 : 135.Type—*Retusanus punctatus* De Long (Mexico).*Rhopalopyx* Ribaut.1939, *Bull. Soc. Hist. nat. Toulouse* 73 : 3.Type—*Jassus preyssleri* Herrich-Schaeffer (Europe).*Rhytistylus* Fieber.1872, *Cat. Eur. Cicad.* p. 10. *Rev. Mag. Zool* 1875 : 117; 1876 : Pl. 12.Type—*Rhytistylus pellucidus* Melichar (1900) (Southern France).*Ribautiellus* Zachvatkin (synonym of *Psamotettix* Haupt).1934, *Mem. Soc. ent. Ital.* 12 : 268.Type—*Deltocephalus pulicarius* Fallen (Italy).*Scaphotettix* Matsumura.1914, *J. Coll. Agric. Sapporo* 5 : 227.Type—*Scaphotettix viridis* Matsumura (Formosa).

Secopennis De Long and Slesman.1929, *Ann. ent. Soc. Amer.* **22** : 855.Type—*Deltoccephalus slossoni* Ball (North America).*Solenopyx* Ribaut.1939, *Bull. Soc. Hist. nat. Toulouse* **73** : 7.Type—*Cicada sulphurella* Zetterstedt (Europe).*Soracte* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* **3** : 55.Type—*Soracte apollonos* Kirkaldy (Queensland).*Sotanus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* **77** : 7.Type—*Athysanus theni* P. Löw (Europe).*Spathanus* De Long.1944, *Bull. Brooklyn ent. Soc.* **39** : 158.Type—*Athysanus acuminatus* Baker (North America).*Spseudotettix* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* **77** : 3.Type—*Cicada subfuscata* Fallen (Europe).*Stenometopiellus* Haupt.1917, *Wien. ent. Zeit.* **36** : 250.Type—*Stenometopiellus sigillatus* Haupt (Bucharra).*Stictoris* Thomson.1869, *Opusc. Ent.* **1** : 51.Type—*Jassus lineatus* Fabricius (Europe).*Stirellus* Osborn and Ball.1902, *Ohio Nat.* **2** : 232, 250.Type—*Athysanus bicolor* Van Duzee (North America).*Streptanus* Ribaut.1942, *Bull. Soc. Hist. nat. Toulouse* **77** : 3.Type—*Cicada sordida* Zetterstedt (Europe).*Synphropsis* Haupt.1926, *Konowia* **5** : 309.Type—*Synphropsis wagneri* Haupt (locality unknown).*Tasmanotettix* Evans.1939, *Pap. Roy. Soc. Tasm.* **1938** : 12.Type—*Tasmanotettix maculata* Evans (Tasmania).*Taurotettix* Haupt.1929, *Zool. Jb.* **58** : 259.Type—*Thamnotettix beckeri* Fieber (Algeria).*Tenuisanus* De Long.1944, *Bull. Brooklyn ent. Soc.* **39** : 73.Type—*Tenuisanus costatus* De Long (Mexico).*Texananus* Ball.1918, *Ann. ent. Soc. Amer.* **11** : 384.Type—*Texananus mexicanus* Ball (Mexico).*Thamnophryne* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* **3** : 61.Type—*Thamnophryne nysias* Kirkaldy (New South Wales).*Thamnotettix* Zetterstedt.1838, *Ins. Lapp.* : 291.Type—*Jassus simplex* Herrich-Schaeffer (= *Cicada prasina* auctt. nec. Fallen).

- Thamnus* Fieber (synonym of *Thamnotettix* Zetterstedt).
1866, *Verh. zool.-bot. Ges. Wien.* 16 : 505.
Type—*Thamnotettix confinis* Zetterstedt (Europe).
- Thomsonia* Signoret.
1879, *Ann. Soc. ent. Fr.* (5) 9 : 51.
Type—*Hecalus kirschbaumi* Stål (Ceylon).
- Thomsoniella* Signoret (new name, invalid, for *Thomsonia* Signoret).
1880, *Ann. Soc. ent. Fr.* (5) 10 : 52.
- Togacephalus* Matsumura.
1940, *Ins. Mats.* 15 : 38.
Type—*Deltocephalus distinctus* Melichar (Formosa).
- Trebellius* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 52.
Type—*Trebellius albifrons* Distant (India).
- Unoka* Lawson.
1928, *Ann. ent. Soc. Amer.* 21 : 451.
Type—*Driotura ornata* Gill (North America).
- Volusenus* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 72.
Type—*Volusenus lahorensis* Distant (North India).
- Yamotettix* Matsumura.
1914, *J. Coll. Agric. Sapporo* 5 : 183.
Type—*Yamotettix flavovittatus* Matsumura (Japan).
- Zioninus* Ball.
1918, *Ann. ent. Soc. Amer.* 11 : 388.
Type—*Phlepsius extremus* Ball (Mexico).

Taxonomic Notes.

During the period when all leaf-hoppers with marginal ocelli were referred to the JASSINAE, this sub-family was usually split into three tribes, the Jassini, Aceucephalini and the Typhlocybini (Lawson, 1920 ; Naudé, 1926). Several authors have recognised further tribes and those proposed by Distant (1908) were both unnatural and misleading. Merino (1930) separated the JASSINAE + ACUCEPHALINAE into the Hecalusaria, Jassusaria, Selenocephalaria, Tartessusaria, Cicadularia, Thamnotettixaria, Athysanusaria and Deltocephalaria. Haupt (1929), while referring the EUSCELINAE, SELENOCEPHALINAE, DELTOCEPHALINAE and GRYPOTINAE to the EUSCELIDAE, recognised the PLATYMETOPIINAE and the CICADULINAE as separate sub-families of the JASSIDAE.

Oman (1934) has divided the EUSCELINAE into the following tribes : Dorycephalini, Hecalini, Selenocephalini, Aphrodini, Cochlorhiini, Xestocephalini, Scaphodiini, Scaphytopiini, Mesamiini, Phlepsiini, Acinopterini, Cicadulini, Deltocephalini, Stirellini, Euscelini and Macrostelini. While the first five of these tribes, in my opinion, belong to other sub-families, only a few of the remainder represent sufficiently well-defined groups to permit comparison with other tribes recognised in this work.

Platymetopiini (fig. 36d-p).

Distribution.

All the principal geographical regions, but in Australia limited to Queensland, with the exception of *Diemoides* (which may be incorrectly placed).

Size, Coloration and General Appearance.

The Platymetopiini range in length from 5 to 10 mm. and in colour are some shade of brown or pale green, often with orange markings. In appearance they are long and narrow and usually have a triangular-shaped crown.

Food-plants and Habits.

Scaphytopius elegans Van Duzee occurs on live oak and *Japanus hyalinus* Osborn on Japanese maple in North America (Ball, 1932b).

Description.

Head. The labium is short or of moderate length and a transverse clypeal suture is sometimes present. The maxillary plates are wide and their outer margins often form an even curve with the genae and the eyes. The antennae are long, the antennal depressions usually shallow, and the antennal ledges are seldom retained. A vestigial epistomal suture sometimes occurs and the frontal sutures diverge posteriorly towards the ocelli; the latter are marginal in position and close to the eyes. The fronto-clypeus is frequently narrowly convex and is often raised into a narrow, median, longitudinal ridge. The frons extends on to the crown and is sometimes bounded posteriorly by a low, transverse ridge, which marks the position of the postfrontal sutures. The crown may be of equal width with the eyes or form a continuous curved surface with the face, but more usually it is flattened and arrow-shaped and at an acute angle with the face. The eyes, which are large, sometimes overlap the pronotum laterally.

Thorax. The pronotum, which is often sparsely pitted, is variable in shape, but most frequently it is wide laterally.

Legs. The hind tibiae are somewhat flattened and curved and a few small spines occur between each of the strongest spines.

Tegmina. The tegmina, which are apically truncate, have either a wide appendix or one of moderate width, and veins R_{1a} and R_{1b} are usually either at right-angles to the costal margin, or reflexed.

Genera comprised in the Platymetopiini.

Acurhinus Osborn.

1920, *Ohio J. Sci.* 20 : 158.

Types—*Dorydium maculatum* Osborn (Guatemala).

Agudus Oman.

1936, *Univ. Kansas Sci. Bull.* 24 : 371.

Type—*Agudus typicus* Oman (Argentine).

Bella Pruthi.

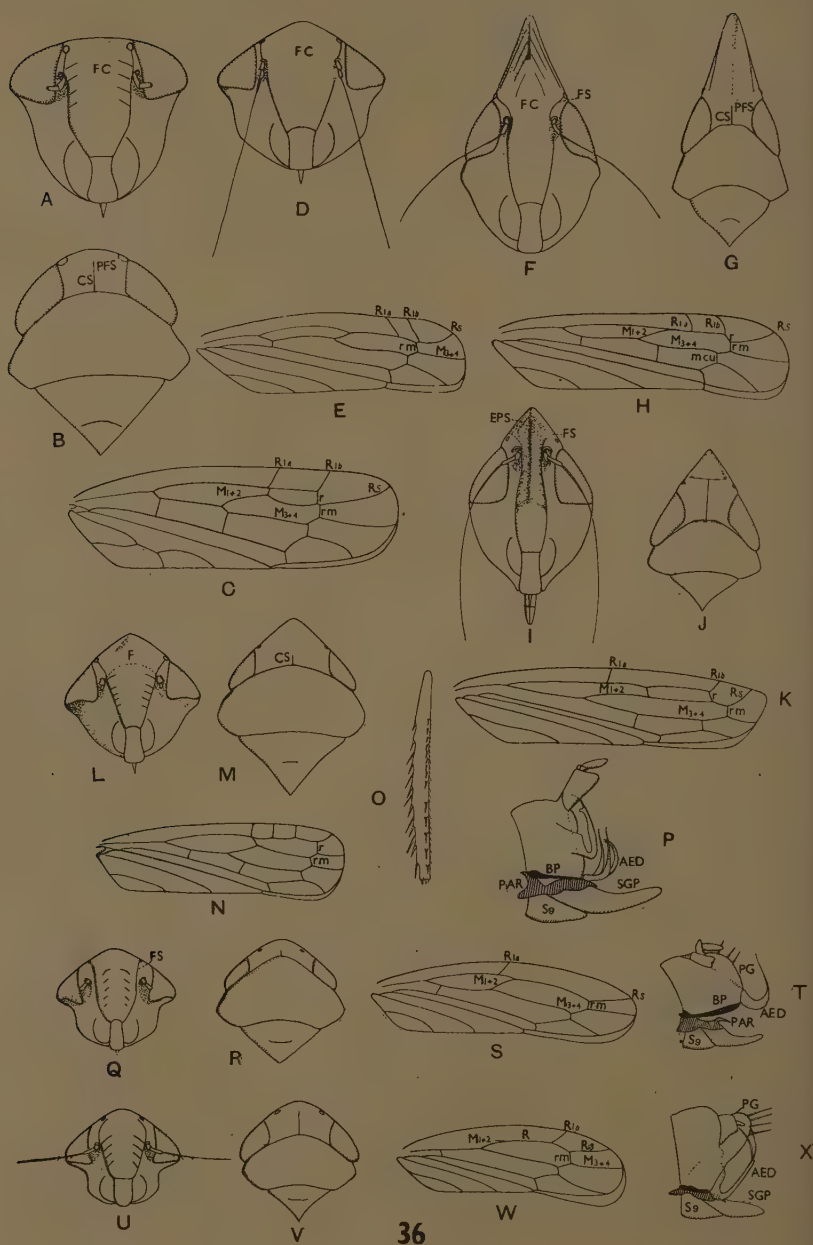
1930, *Mem. Ind. Mus.* 11 : 44.

Type—*Bella apicalis* Pruthi (South India).

Bituitus Distant.

1918, *Faun. Brit. Ind. Rhyn.* 7 : 70.

Type—*Bituitus projectus* Distant (South India).



- Bolanus* Distant (synonym of *Scaphoideus* Uhler).
1918, *Faun. Brit. Ind. Rhyn.* 7 : 89.
Type—*Bolanus baeticus* Distant (Assam).
- Caffretus* Evans.
1947, *Trans. R. ent. Soc. Lond.* 98 : 258.
Type—*Caffretus turneri* Evans (South Africa).
- Calotettix* Osborn.
1935, *Bull. Bishop Mus.* 114 : 247.
Type—*Calotettix metrosideri* Osborn (Marquesas Islands).
- Campbellinella* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 69.
Type—*Campbellinella illustrata* Distant (South India).
- Caphodus* Oman.
1936, *Univ. Kansas Sci. Bull.* 24 : 376.
Type—*Caphodus maculatus* Oman (Argentine).
- Cloanthanus* Ball.
1932, *Canad. Ent.* 63 : 219.
Type—*Platymetopius angustatus* Osborn (North America).
- Convelinus* Ball.
1931, *Canad. Ent.* 63 : 220.
Type—*Platymetopius nigricollis* Ball (North America).
- Coroticus* Distant.
1918, *Faun. Brit. Ind. Rhyn.* 7 : 45.
Type—*Coroticus tessellatus* Distant (Kumaon).
- Deltopinus* Ball.
1931, *Canad. Ent.* 63 : 218.
Type—*Platymetopius nigriviridis* Ball (North America).
- Diemoides* Evans.
1939, *Pap. Roy. Soc. Tasm.* 1938 : 13.
Type—*Diemoides smithtoniensis* Evans (Tasmania).
- Dorydiella* Baker.
1897, *Canad. Ent.* 29 : 159.
Type—*Dorydiella floridana* Baker (North America).
- Dryadomorpha* Kirkaldy.
1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 335.
Type—*Dryadomorpha pallida* Kirkaldy (Queensland).
- Enantiocephalus* Haupt.
1926, *Konowia* 5 : 308.
Type—*Platymetopius cornutus* Herrich-Schaeffer (Europe).
- Garapita* Oman.
1936, *Univ. Kansas Sci. Bull.* 24 : 369.
Type—*Garapita garbosa* Oman (Argentine).

FIG. 36.

A, *Gunghuyana ugandensis* Ev., head ; B, *G. ugandensis*, head and thorax, dorsal aspect ; C, *G. ugandensis*, tegmen ; D, *Platyretus marginatus* Melichar, head ; E, *P. marginatus*, tegmen ; F, *Caffretus turneri* Ev., head ; G, *C. turneri*, head and thorax, dorsal aspect ; H, *C. turneri*, tegmen ; I, *Stymphalus rubrolineatus* Stål, head ; J, *S. rubrolineatus*, head and thorax, dorsal aspect ; K, *S. rubrolineatus*, tegmen ; L, *Platymetopius undatus* de G., head ; M, *P. undatus*, head and thorax, dorsal aspect ; N, *P. undatus*, tegmen ; O, *P. undatus*, hind tibia ; P, *P. undatus*, male genitalia ; Q, *Balchutha punctata* Thunb., head ; R, *B. punctata*, head and thorax, dorsal aspect ; S, *B. punctata*, tegmen ; T, *B. punctata*, male genitalia ; U, *Macrosteles sexnotata* Fall, head ; V, *M. sexnotata*, head and thorax, dorsal aspect ; W, *M. sexnotata*, tegmen ; X, *Macrosteles pallida* Osb., male genitalia.

Giffardia Kirkaldy.1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 386.Type—*Giffardia dolichocephala* Kirkaldy (Queensland).*Grammacephalus* Haupt.1929, *Zool. Jb.* 58 : 258.Type—*Platymetopius pugio* Noualhier (Syria).*Hebenarus* De Long.1944, *Pan-Pacific Ent.* 20 : 41.Type—*Hebenarus pallidus* De Long (Mexico).*Hecaloidella* Osborn.1933, *Ins. Samoa* 2 : 173.Type—*Hecaloidella nitida* Osborn (Samoa).*Hussa* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 68.Type—*Hussa insignis* Distant (South India).*Hybrasil* Kirkaldy.1907, *Bull. Hawaii Sug. Ass. Exp. Sta.* 3 : 41.Type—*Hybrasil brani* Kirkaldy (Fiji).*Japanus* Ball.1931, *Canad. Ent.* 63 : 218.Type—*Platymetopius hyalinus* Osborn (North America).*Kanorba* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 375.Type—*Kanorba reflexa* Oman (Brazil).*Mahalana* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 63.Type—*Mahalana fidelis* Distant (North-West India).*Maiestas* Distant.1917, *Trans. Linn. Soc. Lond. (Zool.)* 17 : 312.Type—*Maiestas illustris* Distant (Seychelles).*Mesamia* Ball.1907, *Proc. Davenport Acad. Sci.* 12 : 59.Type—*Mesamia nigradorsum* Ball (North America).*Nandidrug* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 74.Type—*Nandidrug speciosum* Distant (South India).*Nasutoideus* Ball.1931, *Canad. Ent.* 63 : 212.Type—*Platymetopius nasutus* Van Duzee (North America).*Osbornellus* Ball.1932, *J. Wash. Acad. Sci.* 22 : 17.Type—*Scaphoideus auronitens* Provancher (North America).*Paganalia* Distant.1917, *Trans. Linn. Soc. Lond. (Zool.)* 17 : 314.Type—*Paganalia virescens* Distant (Seychelles).*Paternus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 71.Type—*Paternus pusanus* Distant (Behar).*Platymetopius* Burmeister.1838, *Gen. Ins.* 1 : pl. 14.Type—*Cicada undata* De Geer (Europe).*Platymoideus* Ball.1931, *Canad. Ent.* 63 : 219.Type—*Platymetopius trilineatus* Ball (North America).

Platyretus Melichar.1903, *Homopt. Fauna Ceylon* : 174.Type—*Platyretus marginatus* Melichar (India).*Portanus* Ball.1932, *J. Wash. Acad. Sci.* 22 : 18.Type—*Scaphoideus stigmatosus* Uhler (North America).*Prescottia* Ball.1932, *J. Wash. Acad. Sci.* 22 : 16.Type—*Scaphoideus lobatus* Van Duzee (North America).*Proceps* Mulsant and Rey (synonym of *Platymetopius* Burmeister).1855, *Ann. Soc. Linn. Lyon*. 1855 : 237.Type—*Proceps acicularis* Mulsant and Rey (Southern France).*Pugla* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 318.Type—*Pugla sigillaris* Distant (Tenasserim).*Purpuranus* Zachvatkin.1934, *Mem. Soc. ent. Ital.* 12 : 262.Type—*Platymetopius rubrostriatus* Horvarth (Italy).*Rhombopsis* Haupt.1927, *Zion. Inst. Agric., Nat. Hist. Bull.* 8 : 22.Type—*Rhombopsis virens* Haupt (Palestine).*Sanctanus* Ball.1932, *J. Wash. Acad. Sci.* 22 : 10.Type—*Scapoideus sanctus* Say (North America).*Scaphoideus* Uhler.1889, *Trans. Maryland Acad. Sci.* 1 : 33.Type—*Jassus immistus* Say (North America).*Scaphoidula* Osborn.1923, *Ann. Carnegie Mus.* 15 : 41.Type—*Scaphoidula cingulata* Osborn (Bolivia).*Scaphytopius* Ball.1931, *Canad. Ent.* 63 : 218.Type—*Platymetopius elegans* Van Duzee (North America).*Stymphalus* Stål.1866, *Hemipt. Africana* 4 : 121.Type—*Platymetopius rubrolineatus* Stål (South Africa).*Sunda* Pruthi.1936, *Mem. Ind. Mus.* 11 : 112.Type—*Sunda ribeiroi* Pruthi (India).*Tumeus* De Long.1943, *Bull. Brooklyn ent. Soc.* 38 : 168.Type—*Tumeus serrellus* De Long (Mexico).*Twingingia* Ball.1931, *Bull. Brooklyn ent. Soc.* 29 : 93.Type—*Scaphoideus blandus* Ball (North America).*Varta* Distant.1908, *Faun. Brit. Ind. Rhyn.* 4 : 320.Type—*Varta rubrofasciata* Distant (Bengal).*Viridomarus* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 69.Type—*Viridomarus capitatus* Distant (Calcutta).*Zizyphoides* Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 73.Type—*Zizyphoides indicus* Distant (Calcutta).

Taxonomic Notes.

The position of *Platymetopius* has been discussed by Pruthi (1930), who following Oshanin (1912), Van Duzee (1917) and Osborn (1928) placed this genus in the JASSINAE (=EUSCELINAE) and not in the ACOCEPHALINAE as was done by Melichar (1896). Haupt recognised the distinctive characters of the genus, and in 1929 he erected the sub-family PLATYMETOPIINAE to contain the single genus; later (1935) he gave the group tribal status.

Xestocephalini (fig. 35g-i).*Distribution.*

Universal, apart from the Palaearctic region.

Size, Coloration and General Appearance.

Xestocephalus pulicarius Van Duzee, which is a fairly typical representative of this tribe, is 3 mm. long, and brown in colour with cream-coloured oval markings. Its most noticeable features are its small eyes and evenly rounded crown.

Food-plants and Habits.

X. pulicarius has been recorded from grass (Osborn, 1897) and from *Carex* (Van Duzee, 1923); according to Van Duzee, although this species may occur in dry meadows, it is more especially associated with swampy country.

Description.

Head. The labium is of moderate length and the maxillary plates are wide. The post-clypeus, which is approximately circular in outline, encroaches onto the frontal region as far as the posterior apices of the frontal sutures, and the remnant of the frons, which is triangular in shape, is bounded laterally by the postfrontal sutures. The antennae are long and the second segment is unusually large; the antennal ledges lie alongside the post-clypeus and the antennal depressions are of moderate depth. The crown forms an even curved surface with the face and is evenly rounded anteriorly. Both the eyes and the ocelli are small.

Thorax. The pronotum, which is approximately parallel-sided, is wide laterally.

Legs. The hind tibiae are flattened and all four rows of marginal spines are long and slender.

Venation. The venation may be either complete, or lacking R_{1a} .

Wings. The marginal vein is absent from the apex of the wing.

Genera comprised in the Xestocephalini.

Matsumurana Distant.

1917, *Trans. Linn. Soc. Lond. (Zool.)* 17 : 317.

Type—*Matsumurana facialis* Distant (Seychelles).

Myrmecophryne Kirkaldy (synonym of *Xestocephalus* Van Duzee).

1906, *Bull. Hawaii. Sug. Ass. Exp. Sta.* 1 : 461.

Type—*Myrmecophryne formiceticola* Kirkaldy (Queensland).

Ootacamundus Distant.1918, *Faun. Brit. Ind. Rhyn.* 7 : 57.Type—*Ootacamundus typicus* Distant (South India).*Xestocephalus* Van Duzee.1892, *Trans. Amer. ent. Soc.* 19 : 298.1894, *Bull. Buff. Soc. Nat. Sci.* 197 : 214.Type—*Xestocephalus pulicarius* Van Duzee (North America).*Taxonomic Notes.*

Opinions have varied as to the position of *Xestocephalus*, and while Kirkaldy (1907) regarded it as a relative of *Phrynomorphus*, Van Duzee, Oman (1936) and Medler (1942) have considered it closer to *Acucephalus*. Recently (1943) Oman has recognised the Xestocephalini as a tribe of the EUSCELINAE. *Myrmecophryne* was referred by Kirkaldy to the Cephalellini.

Balcluthini (fig. 36q-t).

Distribution.

Universal.

Size, Coloration and General Appearance.

The Balcluthini range from 3 to 6 mm. in length and in colour are either pink, pale yellow, or green; they are long and slender in appearance and their tegmina overlap apically.

Food-plants and Habits.

Several species of *Balclutha* have been recorded as feeding on grass in Porto Rico (Osborn, 1935).

Description.

Head. The labium is of medium length and the maxillary plates are of moderate width. There is no trace of a separate frons and postfrontal sutures are absent. The antennae are fairly long, the antennal depressions shallow, and the antennal ledges are lacking. The eyes are small.

Thorax. The pronotum may be either wide or narrow laterally.

Legs. The hind tibiae are long and slender and three of the rows of marginal spines are long and slender.

Tegmina. The tegmina are long and narrow and the appendix is moderately wide; sometimes the venation is complete, but frequently that part of R which lies between the base of the tegmen and its junction with M_{1+2} is either indistinct or missing, and R_{1b} is sometimes absent.

Wings. The lower branch of R is fused apically with M_{1+2} .

*Genera comprised in the Balcluthini.**Agelina* Oman.1936, *Univ. Kansas Sci. Bull.* 24 : 392.Type—*Agelina punctata* Oman (Argentina).*Agellus* De Long and Davidson.1933, *Ohio J. Sci.* 33 : 210.Type—*Eugnathodus neglecta* De Long and Davidson (North America).

- Anomiana* Distant (synonym of *Balclutha* Kirkaldy).
 1918, *Faun. Brit. Ind. Rhyn.* 7 : 109.
 Type—*Anomiana longula* Distant (India).
Balclutha Kirkaldy (new name for *Gnathodus* Fieber).
 1900, *Entomologist* 33 : 243.
Balcluthina Pruthi.
 1930, *Mem. Ind. Mus.* 11 : 46.
 Type—*Balcluthina viridis* Pruthi (India).
Baldulus Oman.
 1934, *Proc. ent. Soc. Wash.* 36 : 79.
 Type—*Baldulus montanus* Oman (Arizona).
Eugnathodus Baker (synonym of *Balclutha* Kirkaldy).
 1903, *Invert. Pacif.* 1 : 1.
 Type—*Gnathodus abdominalis* Van Duzee (North America).
Gnathodus Fieber (preoccupied, see *Balclutha* Kirkaldy).
 1806, *Verh. zool.-bot. Ges. Wien.* 16 : 505.
 Type—*Cicada punctatus* Thunberg (Sweden).
Nesosteles Kirkaldy (synonym of *Balclutha* Kirkaldy).
 1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 343.
 Type—*Nesosteles hebe* Kirkaldy (Fiji).
Nesotettix Lindberg.
 1936, *Comment. Biol.* 6 : 6.
 Type—*Nesotettix freyi* Lindberg (Canary Islands).
Pettya Kirkaldy.
 1906, *Bull. Hawaii Sug. Ass. Exp. Sta.* 1 : 343.
 Type—*Pettya anemolua* Kirkaldy (Queensland).

Taxonomic Notes.

Balclutha has been referred by Haupt (1929) to the CICADULINAE, and by Oman (1943) to the BALCLUTHINAE, in both instances these sub-families being distinct units parallel with the EUSCELINAE.

Macrostelini (fig. 36u-x).

Distribution.

Universal.

Size, Coloration and General Appearance.

The Macrostelini range in length from 3 to 4 mm. and in colour they are either pale yellow, or orange, and usually have characteristic, circular, dark brown markings. In general appearance they resemble representatives of the TYPHLOCYBINAE, but differ in the character of tegminal venation.

Food-plants and Habits.

According to Van Duzee (1923) the majority of the North American representatives of this group feed on herbaceous plants; a few, however, feed on shrubs, and *Davisonia major* Dorst is generally taken on *Salix*.

Description.

Head. The face is emarginate beneath the eyes, the labium is of medium length and the maxillary plates are of moderate width. No trace of a separate frons remains and the extent of the frontal region, which is present on the crown, depends upon whether the crown is anteriorly rounded or apically narrow. The antennae are long, the antennal depressions shallow and the antennal ledges not developed. The eyes are large.

Thorax. The pronotum is narrow laterally.

Legs. The hind tibiae bear two rows of long spines.

Tegmina. The venation is almost invariably reduced in a similar manner as in the Balcluthini, that part of R which lies between the base of the tegmen and M_{1+2} being frequently missing, and in addition R_{1a} is often lacking.

Genera comprised in the Macrostelini.

Acrostigmus Thomson (synonym of *Macrosteles* Fieber).

1869, *Opusc. Ent.* 1 : 76.

Type—*Cicada sexnotata* Fallen (Germany).

Cicadulella China (new name for *Cicadulina* Haupt).

1928, *Bull. ent. Res.* 19 : 61.

Cicadulina China.

1926, *Bull. ent. Res.* 17 : 43.

Type—*Cicadulina zeae* China (East Africa).

Cicadulina Haupt (preoccupied, see *Cicadulella* China).

1927, *Zion. Inst. Agric., Nat. Hist. Bull.* 8 : 38.

Type—*Cicadulina pallida* Haupt (Palestine).

Davisonia Dorst.

1937, *Misc. Publ. U.S. Dept. Agric.* 271 : 4.

Type—*Cicadula major* Dorst (North America).

Erotettix Haupt.

1929, *Zool. Jb.* 58 : 255.

Type—*Thamnotettix cyanae* Boheman (Sweden).

Kirotettix Haupt (new name, invalid, for *Cicadulina* Haupt).

1929, *Zool. Jb.* 58 : 255.

Macrosteles Fieber.

1866, *Verh. zool.-bot. Ges. Wien.* 16 : 504.

Type—*Cicada sexnotata* Fallen (Sweden).

Marquesia Osborn.

1935, *Bull. Bishop Mus.* 114 : 250.

Type—*Marquesia atra* Osborn (Marquesas Islands).

Nesolina Osborn.

1935, *Bull. Bishop Mus.* 134 : 60.

Type—*Nesolina lineata* Osborn (Hawaii).

Nesophyla Osborn.

1935, *Bull. Bishop Mus.* 114 : 251.

Type—*Nesophyla picta* Osborn (Marquesas Islands).

Pteropyx Haupt.

1927, *Zion. Inst. Agric. Nat. Hist. Bull.* 8 : 27.

Type—*Pteropyx hyalinus* Haupt (Palestine).

Scaphoidulina Osborn.

1935, *Bull. Bishop Mus.* 114 : 245.

Type—*Scaphoidulina obliqua* Osborn (Marquesas Islands).

Sonronius Dorst.

1937, *Misc. Publ. U.S. Dept. Agric.* 271 : 9.

Type—*Cicadula dahlbomi* Zetterstedt (North America).

Taxonomic Notes.

Owing to confusion in nomenclature this group of genera has at various times been referred to as the CICADULINAE, but the genus *Cicadula* belongs to the Euscelini and should not be associated with *Macrosteles*.

Discussion of the EUSCELINAE.

Although the EUSCELINAE now have a universal distribution and feed on a wide range of food-plants, it is in the Nearctic zone that they are especially well developed, and with grasses that they are particularly associated. As certain representatives, which occur in Western Australia and South Africa, have primitive features which are lacking in the American representatives, it is doubtful whether they will have originated in the last-named country.

Kirkaldy (1906) believed that *Phrynomorphus* represented a primitive type of leaf-hopper, but I hold the opposite view, and consider that the EUSCELINAE represent the culmination of the development of the Macropsides comparable with the TETTIGELLINAE in the Ulopides. As well as having lost all vestiges of maxillary sutures, their antennal ledges are considerably reduced and traces of a distinct frons and of post-frontal sutures are seldom retained. I suggest that this sub-family may have been derived from the JASSINAE by way of a group closely related to the Krisnini.

Some of the Platymetopiini, which are the most highly specialised representatives of the EUSCELINAE, superficially resemble certain of the Aphrodini both in cephalic features and in the venation of the tegmen; however, the heads of insects comprised in the former tribe are not emarginate beneath the eyes, as are so many of the Aphrodini. While the more specialised genera of the Platymetopiini are very distinct from the Euscelini, other genera, such as *Hussa* and *Mesamia*, are intermediate in character.

The position of the Xestocephalini remains problematical; but I consider that this tribe is correctly associated with the Euscelini and that the character of having small eyes may be an adaptive one associated with a former subterranean habit (*Myrmecophryne formeticola* was actually taken in an ants' nest). Finally, the Balcluthini and the Macrostelini are, in my opinion, undoubted Euscelines, which have attained their characteristic features by way of specialisation involving reduction and loss.

Acknowledgements.

In Part I I acknowledged the assistance which had been afforded me by Mr. W. E. China of the British Museum and I mentioned that Mr. China had put at my disposal for use in the present study a list, which he had prepared but never published, of the jassid genera of the world, together with their genotypes. In the preparation of this, the final part of the series, I have again received very considerable assistance from Mr. China, which he has given me ungrudgingly and generously

whenever I have approached him. I am also indebted to Dr. P. W. Oman of the United States Department of Agriculture for arranging for the loan of material from the United States National Museum.

APPENDIX A.

*Genera of Uncertain Position.**Adiaerotoma* Spinola.

1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 99, 170.

Type—*Adiaerotoma eupelicoides* Spinola (Brazil).

Aglenita Spinola.

1852, *Mem. Matem. fis. Soc. Ital. Sci. Modena* 25 : 99, 172.

Type—*Aglenita bipunctata* Spinola (Cayenne).

Diglenita Spinola.

1852, *Mem. Matem. fis. Soc. Ital. Sci. Modena* 25 : 98, 169.

Type—*Jassus peltastes* Burmeister (South Africa).

Discocephalus Kirschbaum.

1858, *Jb. Nassau Verien f. Naturk.* 13 : 356.

Type—*Discocephalus viridis* Kirschbaum (Europe).

Mejunosoma O. Costa.

1834, *Cenni. Zool. (Annuar. Zool.)* : 86.

Type—*Mejunosoma grisea* O. Costa (Italy).

Metapocirtus O. Costa.

1834, *Cenni. Zool. (Annuar. Zool.)* : 85.

Type—*Metapocirtus listatus* O. Costa (Italy).

Pachymetopius Matsumura.

1914, *J. Coll. Agric. Sapporo* 5 : 218.

Type—*Pachymetopius decoratus* Matsumura (Formosa).

Protonesis Spinola.

1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 98, 165.

Type—*Protonesis delegorguei* Spinola (South Africa).

Selenopsis Spinola.

1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 99, 174.

Type—*Selenopsis subaptera* Spinola (Para).

Strongylomma Spinola.

1852, *Mem. Matem. Fis. Soc. Ital. Sci. Modena* 25 : 99, 175.

Type—*Strongylomma caffra* Spinola (South Africa).

Termitopsyllus Wasmann.

1897, *Abh. Senckenb. Ges.* 21 : 169.

Type—*Termitopsyllus purpureus* Wasmann (Madagascar).

APPENDIX B.

Descriptions of New Genera and Species.

Every effort has been made to select named Jassids for illustration purposes, but in a few instances, where the need has occurred to figure a particular structural feature not developed in the available identified material, I have been forced to use unnamed material. The leaf-hoppers for which new names are necessary are described below, with the single exception of the Typhlocybid illustrated in fig. 26c, which I have refrained from describing since no male specimens are available. The types are in the British Museum.

Ulopini.

Caplopa gen. n.

The head is broadly spatulate, the ante-clypeus pear-shaped, the post-clypeus flattened and the antennal pits deep. The antennae lie posterior to the eyes and the frons, which is distinct from the post-clypeus, is entirely ventral in position. The crown, which is extensive and flattened, is approximately rectangular in shape and the ocelli are rudimentary. The pronotum is collar-like and the tegmina, which resemble elytra, narrow apically, and wings are absent. The hind tibiae are short, quadrilateral in section, and have feebly developed spines.

Caplopa turneri sp. n. (genotype) (fig. 1h).

Length 4 mm. General coloration dark brown. *Head* punctate with sparse white hairs on the ante-clypeus and with shallow lateral depressions on the crown. *Thorax* and *tegmen* punctate.

Type ♀ from Cape Town, South Africa (R. E. Turner).

Ledrini

Camptelasmus hyalinus sp. n. (fig. 4b, n).

Length 6.5 mm. *Head* spatulate, the face as wide as long, punctate and pale yellowish-green in colour. Crown medially raised, punctate, pale yellowish-green partially suffused with brown and with two prominent brown markings between the ocelli and the eyes. Ocelli lying anterior to the eyes and nearer to each other than to the margin of the crown. *Thorax* parallel-sided, rugose and raised postero-medially. *Tegmen* hyaline, colourless, with a row of minute prominences lying on either side of every vein. *Thorax* and *abdomen*, ventral surface, pale yellowish-green. *Legs*: hind tibia quadrilateral in section with four rows of marginal spines, of which the three largest are mounted on prominent bases. *Male genitalia* with large, leaf-like, sub-genital plates, long and narrow parameres, and hook-shaped ventrally placed pygophore processes.

Type ♂ from Ceres, Cape Province, South Africa (R. E. Turner).

Ledracephala gen. n.

The head is narrowly spatulate and rugose, the crown is considerably shorter than wide and raised medially, and the ocelli are slightly nearer to each other than to the eyes. The pronotum is rugose, parallel-sided and declivous, and the tegmina, which lack an appendix, have normal jassid venation. The hind tibiae are long and narrow and have two rows of marginal spines, one row of which comprises spines of even length and spacing, and the other row of spines mounted on prominent bases which decrease in size from the apex of the tibia to the base.

Type of the genus, *Ledra brevifrons* Walker, 1851 (fig. 4s). (Distant in 1907 transferred *L. brevifrons* to the genus *Petalocephala* and in 1937a I recorded the fact that this species was not congeneric with the genotype of *Petalocephala* but was a representative of an undescribed genus related to *Rubria*.)

Stenocotini.

Khyphocotis brunneus sp. n. (fig. 5d).

Length 7 mm. *Head*: face black mottled with light and dark brown; crown with a pair of oblique, lateral ridges and a sharp, upturned, anterior rim-like margin, slightly wider against the eyes than in the centre. *Thorax*: pronotum brown, mottled with black in the centre and at the sides posteriorly; scutellum flat. *Tegmen* whitish-hyaline partially

suffused with light and dark brown; veins brown. Venation of the tegmen of the usual jassid pattern apart from the presence of additional costal veins, as Cu_1 , unlike in the majority of the Stenocotini, has only two branches and the anal veins, though linked distally by a cross-vein, each reach as far as the anal border. *Legs*: hind tibiae with four rows of marginal spines, the row mounted on prominent bases comprising only four spines.

Type ♂ from Sydney, New South Wales (J. W. E.).

Paradorydiini.

Paradorydium angolensis sp. n. (fig. 11c).

Length 8 mm.; of the head alone, 4 mm. *Head*: face pale buff with a pair of dark brown lateral stripes which extend from the outer margin of the maxillary plates as far as the apex of the head. Crown and pronotum punctate and rugose, with a median carina extending from the hind margin of the pronotum as far as the apex of the crown. *Tegmen* hyaline, colourless; veins very pale brown, venation complete. *Thorax* ventral surface yellowish, laterally brown. *Legs*: hind tibia quadrilateral in section; both external rows of marginal spines are sparse, irregularly spaced and of equal length.

Type ♀ from Angola, West Africa (T. D. A. Cockerell, viii. 31).

Aphrodini.

Kosmiopelx rieki sp. n. (fig. 12k).

Length 3.5 mm. *Head*: face with a median and posterior lateral depressions, pale brown with brown punctures; antennal depressions dark brown. Crown pale brownish-yellow with evenly distributed brown punctures. *Thorax* pale brownish-yellow with brown punctures on the posterior half. *Tegmen* reduced to half the normal length, whitish, with brown punctures. *Abdomen*: dorsal surface whitish, mottled with brown, the hind margin of every segment brown, and with a median longitudinal brown streak. *Legs*: hind tibia quadrilateral in section and having the two rows comprising the strongest marginal spines widely spaced and of similar length.

Type ♀ from Malooka, Queensland (E. F. Riek).

Postumus hyalinus sp. n. (fig. 12a, b, q).

Length 3.5 mm. *Head*: face dark brown, irregularly mottled with pale brown. Crown arrow-shaped with a median, longitudinal ridge, black, the frontal and coronal sutures white. *Thorax*: pronotum black with three indistinct, longitudinal pale brown stripes. Scutellum black with a median, longitudinal white stripe. *Tegmen*: clavus dark brown, the remainder colourless-hyaline; veins dark brown with restricted white bars. *Thorax* and *abdomen*, ventral surface dark brown. *Legs*: hind tibia narrow, slightly flattened, the spines of the two external marginal rows equally spaced and of approximately equal length.

Type ♂ from Eshowe, Zululand, South Africa (R. E. Turner).

Proconiini.

Phera unipunctata sp. n. (fig. 16n, t).

Length 9 mm. *Head*: face brown, but for a large, oval, buff area on either side of the post-clypeus; post-clypeus medially depressed. Crown brown, the dilator muscle impressions and a few spots buff. *Thorax* parallel-sided, pale brown. Scutellum bright yellow, apically brown. *Tegmen* hyaline, colourless; veins brown.

Type ♀ from Sevilla, Colombia, South America (C. C. Gorwey, v. 26).

IDIOCERINAE.

Chunroides gen. n.

The post-clypeus is slightly convex anterior to the antennae, and the face of the head is flat posterior to the antennae. The frontal and postfrontal sutures are vestigial, but discernible, and the crown forms an even curve with the face. The scutellum is almost as wide as, and considerably longer than, the pronotum. The costal margin of the tegmen is thickened as far as R_{1a} , but R_1 and R_3 are fused together and not separate as in *Chunra*. The hind tibiae are flattened and have three rows of strong spines and a fringing row of hair-like spines; the row comprising the strongest spines contains eight spines.

Chunroides wallabensis sp. n. (Genotype) (fig. 23c.)

Length 6 mm. Head, pronotum and scutellum buff, evenly mottled with pale and dark brown. Tegmen yellowish-hyaline with a wedge-shaped, transverse, white fascia, which is broadest against the anal margin, and with a white area between the arms of R_{1a} and R_{1b} ; veins brown with white bars.

Type ♀ from Essequibo River, British Guiana (*Oxford University Expedition*, xi. 29).

COELIDIINAE.

Sabimoides gen. n.

The head is triangularly produced and apically blunt, the ante-clypeus is wider posteriorly than anteriorly, and the post-clypeus, anterior to the antennae, is flat. The frontal sutures are distinct, and a vestigial epistomal suture occurs in the shape of a narrow inverted V. The crown is medially flat, and the ocelli lie on the sloping sides of the crown, in front of the eyes. The pronotum is extensive and widens posteriorly and the tegmen has typical coelidine venation, similar to that illustrated in fig. 24e. The hind tibiae, which are long and somewhat flattened, have minute spines occurring between each of the strongest spines.

Sabimoides cardamomi sp. n. (Genotype) (fig. 24c.)

Length 8 mm. Head: face brown with five pairs of oval, pale brown muscle impressions between the antennae and the epistomal suture. Crown rugose, pale brown mottled with a dark brown reticulate pattern. Thorax: pronotum and scutellum dark brown with numerous close-set, oval and circular pale brown markings. Tegmen parchment coloured mottled with purplish-brown; veins pale yellow with bold, dark brown bars; Cu_2 , which is distinct from the claval suture, bears several long slender hairs. Abdomen: sternite of the seventh segment in the female dark brown, slightly sinuate, the apex broadly acute.

Type ♀ from Cameron Highlands, Malaya (N. C. Miller on *Elettaria cardamomum*, ix. 37).

NEOCOELIDIINAE.

Chinaia citrina sp. n. (fig. 25a, b, j.)

Length 8 mm. Head yellow, antennae orange, eyes dark brown. Thorax: pronotum medially yellow, the remainder orange. Scutellum orange. Tegmen yellow with transverse and longitudinal orange markings and with two large oval, and a few small brown, markings adjacent to the apex. Thorax, ventral surface yellow. Abdomen, ventral surface orange.

Type ♂ from Essequibo River, British Guiana (*Oxford University Expedition*, ix. 29).

Penthimiini.

Thaumtopoides gen. n.

The face of the head is wider than long and is slightly flexed across the axis of the antennal ledges; the frons is rectangular in shape, and frontal and postfrontal sutures are distinct. The ocelli, which are situated on the thickened margin of the head, between the face and the crown, are slightly closer to the frons than to the eyes. The crown is flat with a shallow antero-median depression and is wider centrally than against the eyes. The pronotum is slightly declivous. The tegmen has complete venation and a wide appendix and the whole of the cubital cell, as well as part of the adjoining cell, forms part of the overfold. The hind tibiae are somewhat curved; minute spines occur between each of the strongest spines, and the spines comprised in the row of longest spines are of variable length.

Thaumtopoides caffra sp. n. (Genotype) (fig. 28a, b).

Length 4 mm. *Head*: lora, ante-clypeus and post-clypeus dark brown; the rest of the face chestnut-brown. Crown and anterior margin of the head pale brown. *Thorax*, pronotum pale brown. *Tegmen* pale hyaline brown; *Legs*: fore and middle legs pale brown, hind legs dark brown, spines buff.

Type ♀ from South-West Africa (R. E. Turner).

Eovulturnops gen. n.

The head is spatulate and the face, which is considerably wider than long, is concave. The antennal ledges are vestigial, and the antennae, which are long, extend beyond the margin of the head, and the vestigial frontal sutures lie parallel with, and slightly above, the antennal ledges. The ocelli lie close to the eyes on a well-defined marginal rim which separates the face from the crown. The crown, which is wide, consists of approximately equal areas of frons and vertex, the two parts being separated from each other by the post-frontal sutures, which together form a wide inverted V. The pronotum is narrow laterally and slightly declivous, and the tegmina, which have wide appendices, have complete venation supplemented by four costal cross-veins lying between R_{1a} and R_{1b} . The hind tibiae are long, and somewhat flattened, and two or three minute spines occur between each of the strongest spines.

Eovulturnops selenocephaloides sp. n. (Genotype) (fig. 28e, f).

Length 5.5 mm. *Head*: face pale brown, crown pale biscuit-colour. *Thorax*, pronotum and scutellum, pale biscuit, irregularly mottled with orange brown. *Tegmen* whitish with reticulate brown mottlings. *Male genitalia*: sub-genital plates basally broad and apically narrow, armed with a series of strong, external marginal spines.

Type ♂ from New River, British Guiana (Hudson, viii. 34).

Auropenthimlia gen. n.

The face of the head, which is more than twice as wide as long, is separated from the crown by a distinct ridge; anterior to this ridge the face lies in two planes situated anteriorly and posteriorly of the antennal ledges. The ante-clypeus is depressed below the level of the post-clypeus, and the latter, except at the sides is flattened. The crown, of which the antennal ledges form the anterior lateral margins, is flat and slightly declivous, and the tegmina, which have complete venation, are shaped as shown in fig. 28i. The hind tibiae are broad, curved, and flattened, and have three rows of long spines; the spines in the row of the longest spines are of variable length and in a few minute spines occur between each of the strongest spines.

Auropenthimia aburensis sp. n. (Genotype) (fig. 28g, h, i).

Length 10 mm., *Head*: face, ante-clypeus, lora and maxillary plates pale brown; post-clypeus chestnut brown with dark brown markings. Crown, pronotum and scutellum chestnut brown. *Tegmen* brown, excepting a white, distal costal area, bordered on either side by dark brown markings. *Thorax*, ventral surface, pale buff, *abdomen* pale brown. The sternite of the seventh segment in the female bilobed, the outer lobe longer and wider than the inner lobe.

Type ♀ from Aburi, Gold Coast, West Africa (1913, *W. H. Patterson*).

Penthimia maculata sp. n. (fig. 28o).

Length 6 mm. *Head* black but for the eyes, ocelli, and the inner margin of the vertex against the eyes, which are brown. Face, posterior to the antennae, evenly convexly rounded, there being no evident separation of the face from the crown. *Thorax*: pronotum declivous, pale brown with a broad, median longitudinal stripe, which widens posteriorly, and two irregular black lateral markings posterior to the eyes. Scutellum black. *Tegmen* with a wide appendix and with the cubital cell and, as well, the adjacent cell which forms part of the overfold, hyaline; irregularly mottled with brown proximally, medially black, with a few large, oval, white areas, and apically colourless; clavus black with brown spots. *Thorax* and coxae black. *Legs* yellow. The seventh sternite in the female with numerous short spines, the inner third black, and the remainder chestnut brown.

Type ♀ from Gendema, Sierra Leone (*E. Hargreaves*, ii. 25).

Gyponini.

Polana draba sp. n. (fig. 30b, d).

Length 6 mm. General coloration chestnut brown. *Head* brown, the crown not sharply separated from the face, with which it forms one curved surface. *Tegmen* with normal complete venation. *Legs*: hind tibia with one or a few minute spines set between each of the strongest spines. *Male genitalia*, pygophores densely covered with long spines.

Type ♂ from Essequibo River, British Guiana (*Oxford University Expedition*, xi. 29).

Selenocephalini.

Drabescus productus sp. n. (fig. 31d, g, j).

Length 7 mm. *Head*: face, maxillary plates, ante-clypeus, the post-clypeus medially, and muscle impressions, chestnut brown; the remainder of the face pale yellowish-brown but for the second antennal segment, which is black. Crown centrally black, bordered with pink and with four round black spots posteriorly placed; the remainder pale yellowish-brown. *Thorax*, pronotum, anteriorly yellowish-ivory bordered with brown, posteriorly grey with brown reticulations and with two irregular black markings medially placed. Scutellum anteriorly yellowish and smooth, posteriorly pinkish and rugose. *Tegmen* pale purplish-brown with long, brown, streak-like markings between the veins; veins dark brown. *Legs*: hind tibia with three rows of long spines, the row containing the longest spines having long and somewhat shorter spines, alternately placed.

Type ♀ from Kuala Lumpur, Malaya (taken on the stem of *Cinnamomum zeylanicum*).

Kutara grisescens sp. n. (fig. 31b, c, h).

Length 8 mm. *Head* buff, mottled with apricot yellow, the post-clypeus slightly convex as far as the hindmost transverse muscle impressions; posteriorly flat. *Thorax*, pronotum khaki brown with small, oval, buff markings. Scutellum lemon yellow. *Tegmen* whitish,

irregularly mottled with two shades of brown; veins pale and dark brown. *Thorax* and *abdomen*, ventral surface lemon yellow. *Legs*: hind tibia pale buff, the enlarged bases of the strongest spines dark brown. *Male genitalia*, sub-genital plates buff, apically dark brown, narrow, and dorsally directed.

Type ♀ from Mt. Poi, 4,350 ft., Sarawak (*E. Mjöberg*).

Jassini.

Jassus leveri sp. n.¹⁶ (fig. 32d, i).

Length 8 mm. *Head* pale green, evenly convex and considerably wider than long; frontal and postfrontal sutures present but indistinct, ocelli nearer to the hind margin of the face than to the postfrontal sutures. Crown distinct from the face, of even width with the eyes. *Thorax*, pronotum and scutellum, pale green, the former slightly declivous. *Tegmen* green but for the apical quarter, which is brown; venation complete and with two additional cross-veins between R_{1a} and R_{1b} . *Legs* with four rows of marginal spines, each row consisting of spines of different lengths. *Male genitalia* as in fig. 32d.

Type ♂ from the Solomon Islands (*R. A. Lever*).

Jassus brunomaculatus sp. n.¹⁶ (fig. 32e, f, h).

Length 6.5 mm. *Head* pale lemon yellow; face evenly convex, distinct from the crown yet forming an even curved surface with it; crown of even width with the eyes. *Thorax*, pronotum pale greenish-yellow with a few irregular brown spots. Scutellum pale greenish-yellow. *Tegmen* hyaline, pale greenish-yellow with evenly distributed, irregularly shaped brown spots; venation complete. *Legs*: hind tibia with three of the four rows of marginal spines comprising spines of equal length and strength.

Type ♀ from Rabai, Kenya, East Africa (*V. G. L. Van Someren*).

Jassus compactus sp. n.¹⁶ (fig. 32g).

Length 5 mm. *Head* pale yellowish-green, eyes red; fronto-clypeus convex, raised above the level of the vertex; ocelli closer to the eyes than to the hind margin of the face. Crown of even width with the eyes, separated from the face by a sharp ridge. *Thorax*, pronotum pale green, declivous. Scutellum rust-coloured with circular white markings. *Tegmen* pale hyaline green with shallow punctures, which give a rugose effect; venation similar to that of the genotype (fig. 32c) in the possession of short apical cells and without the cells adjacent to the appendix forming part of the overfold. *Legs*: hind tibia with four rows of marginal spines, each row comprising spines of different lengths. *Male genitalia* as in fig. 32g.

Type ♂ from South Africa (*R. E. Turner*).

Euscelini.

Gunghuyana ugandae sp. n. (fig. 36a, b, c).

Length 9 mm. *Head*: face pale brown, ocelli large, extending between the apices of the frontal sutures and the sides of the postfrontal sutures as far as the eyes. Crown, pronotum and scutellum orange brown. *Tegmen* hyaline, orange brown, with numerous large, transverse, hyaline white markings; veins, excepting R_{1a} and R_{1b} , which are dark brown, concolorous with the tegmen. *Legs*: hind tibia with three rows of long spines, the row of longest spines consisting of six very long spines alternating with shorter spines, distally placed, and, proximally, eight shorter spines.

Type ♀ from Mitermula, Uganda (*H. Hargreaves*, iv. 31).

¹⁶ While these three new species are undoubted representatives of the Jassini, it is probable that they are not congeneric with *J. lanio*, the genotype of the genus *Jassus*. Their correct generic position will be determined as soon as a study can be made of the jassine genera of the world.

Platymetopiini.

Caffretus gen. n.

The head is narrowly produced, the face convex, and the apex of the face consists of a longitudinal ridge. The crown is flat, and in shape resembles a narrow triangle, the eyes overlap the pronotum laterally, and the ocelli are situated on the margin of the head between the face and the crown, adjacent to the eyes. The pronotum widens slightly posteriorly and the scutellum is extensive. The tegmina are rounded apically and have normal venation with both R_{1a} and R_{1b} recurved. The hind tibiae have minute spines occurring between each of the strongest spines and the spines in the row containing the longest spines are of irregular size.

Caffretus turneri sp. n. (Genotype) (fig. 36f, g, h).

Length 6 mm. *Head*: face pale yellow with brown transverse stripes on the posterior margin. Crown with the apex reddish-brown laterally, the centre dark brown, the remainder dark brown with pale brown markings arranged in a symmetrical pattern. *Thorax*, pronotum and scutellum coffee colour with small oval whitish spots and five incomplete, longitudinal, narrow white spots. *Tegmen* brown, the costal border broadly white, apart from R_{1a} and R_{1b} which are brown. *Thorax*, ventral surface, and *legs* pale yellow, but for the episterna of the mesothorax, which are dark brown.

Type ♀ from Okahandja, South Africa (*R. E. Turner*).

New Names.

The following new generic names have been proposed in the preceding pages to take the place of preoccupied names:

Tettigellini.

Anchuralia, new name for *Anchura* Melichar (p. 159).

Apogonalia, new name for *Apogonia* Melichar (p. 159).

Catagonalia, new name for *Catagonia* Melichar (p. 160).

Cephalogonalia, new name for *Cephalogonia* Melichar (p. 160).

Eugonalia, new name for *Eugonia* Melichar (p. 161).

Paragonalia, new name for *Paragonia* Melichar (p. 163).

MELICHARELLINAE.

Bergevina, new name for *Macroceps* Melichar *nec.* Signoret (p. 189).

TARTESSINAE.

Stenotartessus, new name for *Euprora* Evans (p. 207).

HYLICIDAE.

In Part 2 (*Trans. R. ent. Soc. Lond.* 97: 47) the type of *Parasudra*, Schmidt was given as *P. borneensis* Schmidt, from North Borneo. This was an error, as the type of *Parasudra* is *sumatrana* Schmidt from Sumatra. *Melliola* Hedicke was incorrectly given as *Melliala* and the following genus omitted.

Pseudosudra Schmidt.

1919, *Archiv. Naturg.* 85a: 118.

Type—*Pseudopsudra borneensis* Schmidt (North Borneo).

EURYMELIDAE.

The following genus, which belongs to the sub-family IPOINAE, was omitted from the list of genera given on p. 52 of Part 2.

Stenipo Evans.

1934, *Trans. Roy. Soc. S. Aust.* **58** : 155.

Type—*Stenipo swani* Evans (Western Australia).

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ABBREVIATIONS USED IN FIGS. 1-36.

AC. anteclypeus ; AED., aedeagus ; AL. antennal ledge ; ATP., anterior tentorial pit ; BP. basal plate ; CS., coronal suture ; EPS., epistomal suture ; F., frons ; FS., frontal suture ; L., lorum ; MP., maxillary plate ; MS., maxillary suture ; Oc., ocellus ; PAR., paramere ; PC., post-clypeus ; PN., pronotum ; S9., ninth sternite ; SGP., subgenital plate.

INDEX TO THE GENERA OF THE JASSOIDEA (WITH THE EXCEPTION OF THE MEMBRACIDAE).

(Those genera comprised in the AETALIONIDAE, HYLICIDAE and EURYMELIDAE are indicated by an A, H, and E respectively, and the corresponding page numbers refer to Pt. 2 in this series.)

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THE ORIGIN AND HISTORY OF THE
BRITISH MACRO-LEPIDOPTERA

By BRYAN P. BEIRNE, PH.D., M.R.I.A., F.R.E.S.

Manuscript received 31st December, 1946

(Read 4th June, 1947)

WITH 45 MAPS

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INTRODUCTION

COMPARATIVELY little has been published previously on the questions of how and when each species of Lepidoptera first became established in the British Isles, on the histories of the species subsequent to their establishments, on why each species has its own particular type of distribution, or on why many species are represented by local races in the British Isles. Until recently, one of the many complex problems involved in an investigation of these points was the difficulty of obtaining full information on the nature and extent of past climatic and vegetational changes. This problem has been greatly simplified by the publication of several recent works which summarise and correlate the geological information; those of Movius (1942) and Zeuner (1945, 1946) are of particular importance in this respect. It is now possible to reconstruct tentatively the history of the British lepidopterous fauna as far back as some 120,000 years ago. This is what has been attempted here and it must be regarded merely as a preliminary survey of the subject. When more information, particularly on the species' ecology, becomes available it should be possible to reconstruct the histories with a greater degree of probable accuracy than can be done at present. Naturally, most of the conclusions arrived at here are largely theoretical, as fossil remains of existing species of Lepidoptera are virtually unknown in the British Isles. Nevertheless this paper may be of some value, as no detailed study of the origin and history of any large non-fossil group of the British fauna or flora has been published previously.

An incidental result of this study was that the Lepidoptera provided some indication, additional to that provided by geological evidence, of the composition of the flora of parts of the British Isles at certain times in the past, of the positions of former coast-lines of north-western Europe, and of the rate of evolutionary change in these insects.

II. ACKNOWLEDGEMENTS.

The manuscript has been read by Mr. E. P. Wiltshire, to whom I wish to express my sincere thanks for his criticisms and constructive suggestions. The nomenclature used here is that given in Kloet and Hincks' *Check List of British Insects* (1945), with a few corrections for which I am indebted to Mr. T. Bainbrigg Fletcher and Mr. W. D. Hincks. I also wish to thank Professor G. D. Hale Carpenter, who has read part of the typescript; Mr. G. F. Mitchell, for assistance on geological matters; Mr. A. J. Wilmott, for botanical information; Mr. R. B. Benson; and Mr. J. F. Bird, Herr A. G. Carolsfeld-Krause, Dr. E. A. Cockayne, Dr. E. B. Ford, Mr. T. Greer, Professor J. W. Heslop Harrison and Mr. Austin Richardson for assistance with entomological information.

III. THE MODE OF ARRIVAL.

There are a few species of Lepidoptera which do not appear to have been found outside the British Isles, for example *Hydraecia paludis* Tutt, *Dysstroma concinnata* Stephens, *Oporinia christyi* Prout, *O. umbrifera* Prout and *O. scotica* Cockayne. Each is easily confused with its allies and, in most cases, has been recognised as a good species only comparatively recently. As they passed unrecognised for so long in the British Isles—where the Lepidoptera have been studied far more intensively than in other countries—it is reasonable to assume that they have yet to be recognised abroad and unlikely that any is an endemic British species. The remaining 809 resident species have all been found abroad and with a single exception they all occur on the European mainland.

No species has a distribution which would indicate that it developed in the British Isles and spread thence to the European mainland, although there are several subspecies which may have had this history. Thus it may be concluded that all the species now inhabiting the British Isles spread originally into the country from abroad. They could have arrived in three ways: by human agency, by overseas flight, or by spreading over land-connections which no longer exist.

(a) *Establishment by Human Agency.*

Colonies of several non-British species of Lepidoptera have been established deliberately in the British Isles and there is a larger number of species which probably became established by accidental importations with their foodplants.

The best-known example of a deliberate establishment is that of *Lycaena dispar* Haworth. Originally an indigenous species (see p. 304), it became extinct in 1847 or 1848 and was successfully re-established in the Fenlands in 1927, after an earlier, temporarily successful, establishment in Tipperary. *Euplagia quadripunctaria* Poda (*hera* L.) apparently was introduced into Devonshire from the Channel Islands about 1865 and still survives there.

It is likely that all or most of the Gooseberry- and Currant-feeding species were added to the British fauna by accidental importations. They include *Eupithecia assimolata* Guenée, *Lygris prunaria* L. (*ribesaria* Boisduval), *L. mellianata* Fabricius (*associata* Borkhausen), *Itama wauaria* L. and *Aegeria tipuliformis* Clerck. The same applies to most of the conifer-feeding species, with the exception of the Juniper- and certain of the Spruce-feeders. They include *Panolis griseovariegata* Goeze (*piniperda* Panzer, *flammea* Hübner), *Eupithecia lariciata* Freyer, *E. indigata* Hübner, *Eucymatoge pini* L. (*togata* Hübner), *Semiothisa liturata* Clerck, *Thera obeliscata* Hübner, *T. firmata* Hübner, *Ellopija prosapiaria* L. (*fasciaria* Schiffermüller, *prasinaria* Schiffermüller) and *Bupalus piniaria* L. All these must have been artificially introduced into Ireland as there is no evidence that their food-plants have survived there since pre-historic times. It is possible, however, that some of them survive as natives in the Scottish Highlands (see p. 309), but all must have been artificially spread over the greater part of their ranges in Great

Britain. There is some evidence that *E. lariciata* and *E. pini* were not natives. Neither was found in the British Isles before the middle of the nineteenth century, although both now occur in all parts of the country.

At least three species which are natives of England must have been artificially introduced into Ireland as their food-plants are not indigenous in the latter country. They are the Beech-feeding *Cosymbia trilinearia* (see p. 348), and the Clematis-feeding *Hemistola immaculata* (p. 348) and *Eupithecia isogrammaria* (p. 348).

(b) *Establishment by Overseas Migration.*

Intermediate between the non-resident species of Lepidoptera found occasionally or regularly in the British Isles and the permanent residents are several species which arrive by overseas migration and establish themselves for shorter or longer periods but eventually die out, to re-establish themselves at later dates. Probable examples are *Nyctosea obstipata* Fabricius (*fluviata* Hübner, *gemmata* Hübner), *Aplasta ononaria* Fuessley, *Ennomos autumnaria* Werneburg, (*alniaria* Schiffermüller nec L.) and *Cyaniris semiargus* Rottenburg. At least one species has established itself as a permanent resident by overseas migration within recent times. This is *Polychrisia moneta* Fabricius which was not found in the British Isles before 1890, but has since spread over most of Great Britain, reaching Ireland in 1939. *Hyloicus pinastri* L. may be a parallel case, but there is a possibility that it was accidentally imported with its food-plant, pine.

Many of the permanent residents are known or suspected immigrants and it is apparent that they could have become established in the British Isles in the first instance in this way, like *P. moneta*. For this reason it is often not possible to reconstruct their early histories as British species with any degree of confidence, and with a few exceptions they are not discussed in subsequent chapters. The suspected migrants are as follows (see also p. 357):

Eilema pygmaeola Doubleday (see p. 304).

Lithosia quadra L.

Hypocrita jacobaeae L.

Spilosoma lutea Hufnagel (*lubricipeda* auctt. nec L.).

S. lubricipeda L. (*menthastri* Esper auctt.).

Amphipyra tragopogonis L.

Luperina testacea Schiffermüller.

Nonagria dissoluta Treitschke (*neurica* Duponchel nec Hübner).

Cosmia trapezina L.

Rhizedra lutea Hübner (*crassicornis* Haworth).

Arenostola pygmina Haworth (*fulva* Hübner).

A. phragmitidis Hübner.

Phlogophora meticulosa L.

Xylophasia monoglypha Hufnagel (*polyodon* L. nec Clerck).

Celaena secalis L. (*nictitans* Esper nec L., *didyma* Esper, *oculea* Guenée nec L.).

Procus strigilis Clerck.

Euxoa tritici L. (see p. 302).

Agrotis segetum Schiffermüller.

Scoliopteryx libatrix L.

Emmelia trabealis Scopoli (*sulphuralis* L.).

Plusia gamma L.

Lymantria dispar L. (see p. 304).

Euproctis chrysorrhoea L. (*similis* Fuessly).

Leucoma salicis L.

Sterrhia aversata L.

S. emarginata L.

Scopula imitaria Hübner.

- Scopula rubiginata* Hufnagel (*rubricata* Schiffermüller).
Eupithecia centaureata Schiffermüller (*oblongata* Thunberg).
Euphyia bilineata L. (see p. 342).
Xanthorhoë montanata Schiffermüller (see p. 342).
Opisthograptis luteolata L. (*crataegata* L.).
Chiasmia clathrata L.
Lycia hirtaria Clerck.
Abraaxas grossulariata L. (see p. 312).
Crocata gilvaria Schiffermüller.
Cabera exanthemata Scopoli.
Agrotis ypsilon Rottenburg (*lunigera* auctt, nec Stephens, *suffusa* Hübner).
A. exclamationis L.
Actebia praecox L.
Amathes c-nigrum L.
A. xanthographa Schiffermüller.
Diarsia rubi Vieweg (*bella* Borkhausen).
Triphaena pronuba L.
T. comes Hübner (*orbona* Fabricius nec Hufnagel) (see p. 341).
T. orbona Hufnagel (*subseque* Schiffermüller) (see p. 334).
Aporophyla australis Boisduval (see p. 297).
Anchoscelis lunosa Haworth.
Cirrhia gilvago Schiffermüller.
Cucullia asteris Schiffermüller.
Graptolitha furcifera Hufnagel (see p. 316).
Leucania vitellina Hübner.
Hadena bicruris Hufnagel (*capsincola* Schiffermüller).
H. chenopodii Schiffermüller (*trifolii* Rottenburg).
Mamestra brassicae L.
Ourapteryx sambucaria L.
Selenia bilunaria Esper (*illunaria* Hübner).
Deuteronomos alniaria L.
Crocallis elinguaris L.
Macroglossum stellatarum L.
Acherontia atropos L.
Lophopteryx capucina L. (*camelina* L.).
Leucodonta bicoloria Schiffermüller (see p. 315).
Pararge megera L.
Maniola jurtina L. (*janira* L.) (see p. 318).
Coenonympha pamphilus L.
Nymphalis io L.
Lycaena phlaeas L.
Pieris brassicae L.
P. rapae L.
P. napi L. (see p. 312).
Papilio machaon L. (see p. 304).
Malacosoma neustria L.
Gastropacha quercifolia L.

With fourteen exceptions any of the remaining resident British species of Macrolepidoptera could have become established by overseas migration from abroad. The exceptions are the species whose females have only rudimentary wings and are thus incapable of flight. However, there are good reasons for believing that the great majority of the remainder did not become established in this way. One reason is that most of them never have been suspected of possessing migratory habits. At present only about eighty of the 814 resident species are known or suspected migrants, and while there is little doubt that this figure will be increased by future observations it seems improbable that it will ever come to include the majority, or even as much as one-fifth, of the total number. A second reason is that a great many species have feeble powers of flight or sedentary habits and never have been found far from their breeding-grounds, rendering it unlikely that they could have covered the considerable stretches of sea separating the British Isles from the Continent. Furthermore a large number of the species which inhabit western Europe never have been taken in the British Isles and a large number of those which occur in Great Britain never

have been taken in Ireland. If they possessed migratory habits they might be expected to occur, at least occasionally, in the regions in which they do not occur as residents. A very important reason is that a considerable number of species are represented by endemic subspecies or races in the British Isles, which indicates that they have long been established without any interbreeding with new arrivals from abroad and therefore that immigration is, and has been for a long time, a negligible factor. Then there is the fact that the distributions of a great many species are not such as might be expected to result from the establishment of immigrants—they are absent from those parts of the country which they might be expected to reach first if they flew from the Continent and their distributions can be explained readily if overland migration is assumed. Many of them have distributions similar to those of species whose females are incapable of flight, and thus may have had similar histories.

(c) *Establishment by Overland Migration.*

The chief reason for concluding that the great majority of the British species of Macrolepidoptera spread into the different islands of the British Isles over land-connections which no longer exist, rather than by overseas migration, is that it is known that such land-connections existed for long periods in the past. While there are many objections to establishment by overseas migration there are none to establishment by spreading into the country over land. Most of the existing flora of the British Isles must have arrived in this way and it must have been accompanied by its associated Lepidoptera.

Extensive changes in the relative levels of land and sea took place during the Pleistocene Ice Age, which lasted for some 600,000 years, ending about 22,000 years ago. These changes were caused in two ways. Most important were eustatic changes in the sea-level: changes in the general level of the sea due to the repeated absorption and release of water as the ice-sheets expanded and contracted. Thus periods of glacial advance were periods of falling sea-level, while the level rose as the ice retreated. Estimates of the extent to which the sea-level was lowered vary. Zeuner (1945, 1946) concluded that it was at least 300 feet below its present level during the last of the four Pleistocene glaciations, while Farrington (1945) estimated it at considerably more than 400 feet. Even taking a conservative estimate of 300 feet it is apparent that during most of the Pleistocene the British Isles must have formed part of the European land-mass (see fig. 3). It was not until several thousand years after the final disappearance of the ice from the British Isles that the sea had risen approximately to its present level. It is obvious that the Lepidoptera could have spread to all parts of the British Isles over land during and following the Pleistocene period.

Changes in the relative levels of land and sea also resulted from isostatic movements of the land. The enormous weight of an ice-sheet caused the land immediately under and around it to sink, and on the disappearance of the ice the land rose once more. Such movements,

however, were of comparatively little importance to the history of the British Lepidoptera. They were only local in their occurrence, while eustatic changes in the sea-level were world-wide.

It is reasonable to conclude, therefore, that the great majority of those species of Lepidoptera which are not known or suspected migrants became established in the British Isles in the first instance by spreading over the former land-connections. The way in which the probable age and history of each species as an inhabitant of the British Isles can be reconstructed can now be explained briefly.

IV. THE RECONSTRUCTION OF THE HISTORIES.

As land-connections between the British Isles and the Continent were in existence for perhaps hundreds of thousands of years in the comparatively recent past and as the British fauna includes species characteristic of a great variety of types of climate and habitat it is apparent that all the Lepidoptera did not invade the country at the same time. Rather, there was a continuous succession of invasions extending over a long period of time. Three types of evidence may be utilised in reconstructing the age and the history of each species: ecological, taxonomic and zoogeographical. One type by itself is rarely of much value, but with most species the history indicated by one type of evidence is confirmed by another or by both others.

(a) *Ecological Evidence.*

If both the nature of the ecological factors which regulate a species' distribution at the present day and the extent of their occurrence at different times in the past are known, then the species' probable distribution and abundance at the different times in the past could be reconstructed by comparing the one with the other. In theory the species' histories could be reconstructed most easily in this way, but the difficulty is that at present little is known of the ecology of the majority. However, the distribution of each species is known fairly accurately and by comparing it with climatic data the identities and nature of the climatic factors which regulate it may often be surmised. More importantly, the habitats of each species are known and there is a considerable amount of information available on the distribution of different types of vegetation in the past. Consequently it is sometimes possible to arrive at tentative conclusions from evidence of this type.

(b) *Taxonomic Evidence.*

Few groups of animals or of plants exhibit local variation to the same extent as do the Lepidoptera, a fact which enables the histories of these insects to be reconstructed with a correspondingly greater degree of probable accuracy. Races, subspecies and clines are the types of variation which are important in this respect.

Subspecific variation normally may be taken as indicating that the population exhibiting the variation was isolated from other populations

of the species for a long period of time, during which it developed independently. Frequently, however, the ranges of two subspecies of the one species meet or overlap and interbreeding may take place. In such cases it may be assumed that the ranges of the two came together at a comparatively recent date as a result of distributional changes on the part of one or both. In dealing with the British Lepidoptera it usually may be concluded that the two subspecies represent different invasions of the country. Incidentally this usually is confirmed by zoogeographical or ecological evidence. When two subspecies occur in different parts of the country, however, it is often difficult to judge whether they represent separate invasions or are the survivors of the same invasions and have developed independently as a result of their isolation from each other.

Variation in the form of a cline—a gradual change in characters from one region to another over a large area—may be taken to indicate that the species has been long established in the region in which the variation occurs.

The term “race” refers to any population of a species which differs taxonomically or in habits from populations found elsewhere. It includes subspecies but is used here mainly in referring to stages in a cline or to populations which have distinctive habits but which do not differ taxonomically to any marked degree from other populations. Racial variation in habits normally may be taken to indicate that the population exhibiting the variation was subjected to some ecological change which forced it to change its habits and which did not affect other populations of the species.

(c) Zoogeographical Evidence.

While taxonomic evidence may indicate the age of a species as an inhabitant of a region and ecological evidence its probable abundance at different times in the past, the chief evidence on which the species' histories may be constructed usually is provided by their ranges and distributions. A distinction must be made between these two terms. As used in the following chapters, the term “range” refers to the total area of a country within which a species is found, irrespective of whether the species occurs everywhere within that area or only in a few widely-separated localities. The term “distribution” refers to the species' occurrence within its range.

A restricted range may mean that a species is a comparatively recent arrival or it may mean that it had a wider range at some time in the past, this range later being reduced by the onset of unfavourable ecological conditions. If taxonomic or ecological evidence do not indicate which was the case with a particular species, the situation of the area within which the species is found compared with past ecological changes and the sites of former land-connections usually provides information on the species' probable history.

A discontinuous distribution, when not due to artificial importations or the establishments of migrants, normally indicates some degree of

relative antiquity. At some time in the past a species having this type of distribution must have occurred in or spread over the regions between the areas in which it now occurs, but was later exterminated in those regions by the onset there of ecological conditions which were unfavourable to it. Here, as with the species which have restricted ranges, a comparison between the species' ecology and the ecological changes which have taken place in the past often indicates the date at which the distribution became discontinuous, or the range restricted.

A distribution which is general, or at least not very local, throughout a species' range usually indicates that the species was a comparatively recent arrival whose range and distribution have not undergone any important reductions since its establishment. There are exceptions to this: species for which a greater degree of antiquity is indicated by ecological or taxonomic evidence or by their types of ranges.

Finally, the occurrence of species in certain islands may be important in indicating their histories as British species as the date at which the former land-connections between those islands and other lands were severed may be known. It is apparent that all the non-migratory species of Lepidoptera must have arrived in such an island while it was still connected to other countries.

(d) The Sequence of Arrivals.

As far as possible the species are discussed in the following chapters in accordance with their probable ages as inhabitants of the British Isles, the oldest inhabitants being dealt with first. As mentioned above, the Lepidoptera became established in the British Isles by a succession of invasions extending over a long period of time. This succession of invasions may be divided into six main periods, or waves of immigration. The evidence set forth in the following chapters indicates that species characteristic of cold climates invaded the country in three distinct waves, separated from each other by long periods during which species characteristic of more temperate climates arrived. There were undoubtedly earlier waves of immigration, but these six are the only ones for which there is good evidence.

The six main waves of immigration correspond with known past climatic changes. The most recent immigrants, whose descendants are now the dominant species over most of the British Isles, were species characteristic of cool temperate and temperate climates, a few of them being characteristic of a climate which must have been rather warmer than that of the present day. These must have been postglacial arrivals. The preceding wave of immigration, which was by species characteristic of cold climates, may then be correlated with the most recent of the three glacial phases of the last, or Upper Pleistocene, glaciation, the two earlier invasions of cold climate species with the first and second glacial phases and the two earlier invasions by temperate climate species with the two interstadial phases. Of the latter, the first invasion was far more important than the second and included species characteristic of a climate which was rather warmer than that of the present day. This

agrees with our knowledge of the interstadial phases : the first was long and the climate was at least as warm as that of the present day, while the second was relatively very short and the climate probably was not so mild as at present. The evidence for these correlations is discussed in greater detail in the following chapters.

Thus, with a few possible exceptions, we cannot at present reconstruct the history of any species of Lepidoptera as an inhabitant of the British Isles farther back than the beginning of the last of the four main glaciations of the Pleistocene. This does not mean that no species has inhabited the country since an earlier period. Many probably are very ancient inhabitants, some possibly dating from pre-glacial (Pliocene) times. The earlier survivors all were reinforced by subsequent invasions of the same species, in Upper Pleistocene or in postglacial (Holocene) times, many of them being reinforced on two or more occasions. With such species evidence of only the most recent or two most recent invasions exists, so that it is at present not possible to conclude which have survived from earlier dates. The number of Pliocene and early Pleistocene survivors probably is small, as most of the species which arrived during the earlier glaciations probably became extinct in the British Isles during the long and warm Third Interglacial period and most of the Pliocene and interglacial arrivals probably became extinct during the first glacial phase of the Upper Pleistocene.

V. THE EARLY UPPER PLEISTOCENE ARRIVALS.

The species discussed here are those which probably arrived in the British Isles during the first glacial phase of the Upper Pleistocene glaciation, together with a few possible survivors from the last interglacial period.

(a) *The Interglacial Survivors.*

The last interglacial period was of about 60,000 years' duration and the climate was partly warmer than that of the present day. At that time the British Isles must have been inhabited by an extensive lepidopterous fauna, but this fauna has been so greatly modified and obscured by later climatic changes and by subsequent invasions that little trace of it survives.

In the case of *Hadena caesia* Borkhausen, *H. andalusica* Staudinger and *H. lepida* Esper there is some slight evidence indicating survival since interglacial times. They have mainly southerly ranges on the Continent and thus must have invaded the British Isles during one or more of the temperate climatic periods of the past, rather than during any of the glacial phases. For reasons which will be explained in the next chapter there are good reasons for believing that they date from the first interstadial phase as inhabitants of Ireland. In the south-west of Ireland varieties occur which are similar to Spanish forms of the species and which may represent the remnants of an earlier invasion. They are the form *nigrescens* Staudinger of *H. caesia*, which also occurs in

the Pyrenees, the form *andalusicidea* Donovan of *H. andalusica*, which is similar to the typical subspecies found in the mountains of Spain, and the form *suffusa* Tutt of *H. lepida*, which corresponds to Guenée's var. A from Spain (Donovan, 1936). It is apparent from their distributions abroad that if these "Lusitanian" forms do represent distinct invasions from the ordinary Irish subspecies then they must have arrived at a time when the climate was warmer than now. This was the case during the last interglacial period. Furthermore their Irish distributions indicate that they were inhabitants of the now-submerged glacial land south of that country—a region to which they would have been confined if they had survived the first glacial phase in the British Isles.

Other possible interglacial survivors are the race *flavicans* Boisduval of *Setina irrorella* Clerck, which represents the species in the Burren area of western Ireland and in the Mediterranean region, the form *iberica* Staudinger of *Xanthorhoe montanata* Schifferrmüller, which is found at high altitudes in the mountains of south-west Ireland and of Castile and Andalusia, Spain (Donovan, 1936), and the small Irish race of *Selidosema plumaria* Schifferrmüller, which, according to Barrett, is similar to a form found in southern Spain. The second of these is the form which is most likely to be of interglacial age; the other two more probably were first interstadial arrivals.

(b) *The First Glacial Phase of the Upper Pleistocene.*¹

At their maximum, some 115,000 years ago, the ice-sheets of the first glacial phase of the last glaciation were considerably more extensive in the British Isles than those of the second and third glacial phases and apparently were at least as extensive as those of any earlier glaciation. The only ice-free areas in what are now the British Isles were England south of the Severn and Thames and the extreme south-west of Ireland (see fig. 1), but owing to the great eustatic lowering of the sea-level there must also have been extensive areas of ice-free land off the present south coasts. On the Continent immense ice-sheets covered Scandinavia as far south as northern Germany² and radiated out from the Alpine region (see fig. 2). During this glacial phase Lepidoptera invaded the British Isles from three directions. Firstly there were one or two species which may have arrived from a northerly or north-westerly direction. Secondly there were the species which originally inhabited northern Europe and were driven southwards by the advancing ice into north-central Europe, whence they spread westwards into southern England along the tundra and sub-arctic zones south of the ice-fronts. And thirdly there were species which originally inhabited the mountains of central Europe and which also were driven down into north-central Europe by the ice—in this case the Alpine ice—and spread westwards into the British Isles.

¹ Also known as the Old Drift (in part), The Third Pleistocene Glaciation of Ford (1945), the Second Pleistocene Glaciation of Stamp (1946).

² The Warthe glaciation.

³ The Würm I glaciation.



FIGS. 1 and 2.—Probable maximum extent of the Upper Pleistocene ice-sheets on the present land-area: 1, in the British Isles (semi-diagrammatic, partly after Movius, 1942); 2, in Northern and Central Europe (redrawn, after Zeuner, 1946).

(c) The "American" Species.

Xylophasia exulis Lefebvre is a species which must have arrived in the British Isles from a northerly direction as it is not found on the mainland of Europe, although a closely-related species, *A. maillardi* Geyer, occurs there. *X. exulis* inhabits tundra regions in Labrador, Greenland, Iceland, Spitzbergen and the Faroes and is found on the mountain peat-bogs in the Shetlands and in Scotland. It must have reached Scotland from Iceland or the Faroes over a former land-connection.

The composition of the lepidopterous faunas of the North Atlantic islands indicates that at some time in the past a land-connection extended between Europe and America, over which Lepidoptera spread both eastwards and westwards (Beirne, 1945). At a much later date a land-connection extended from Europe to Iceland and the Faroes only (*loc. cit.*), this being indicated by the fact that the lepidopterous faunas of those islands are predominantly European in composition. The latter land-connection probably was in existence up to at least the first glacial phase of the Upper Pleistocene. This is indicated by most of the Lepidoptera of Iceland and the Faroes showing no taxonomic evidence of having inhabited those islands for a longer time than the first glacial and certain of the first interstadial phase species have inhabited the British Isles. The eustatic lowering of the sea-level, although extensive, probably was not sufficient to result in the appearance of such a land-connection at that time, even taking into account the fact that the

submarine ridge which now extends from Scotland to Iceland via the Faroes (see fig. 3) must have had its height considerably reduced by erosion. Wegener's theory of continental drift—that large-scale horizontal movements of the continents on the earth's crust have taken place—provides a more reasonable explanation for the existence of the land-connection. It seems to be generally agreed that horizontal movements of the continents have occurred, and are still in progress at the present day, but there is disagreement as to their intensity and rate (Zeuner, 1946). Wegener suggests that the separation of Greenland

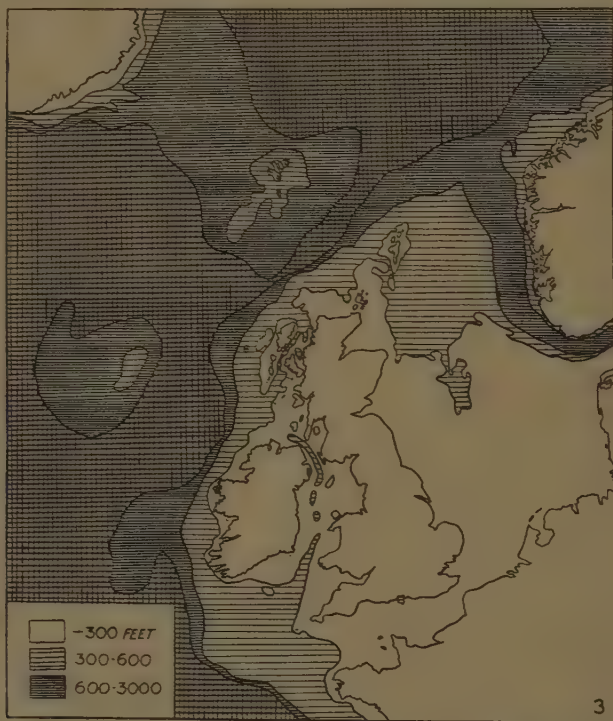


FIG. 3.—Present depths of sea around north-western Europe, indicating the approximate positions of the Pleistocene coast-lines.

from Scotland took place as recently as the Upper Pleistocene. Apart from Wegener's evidence for so recent a separation being open to question, the distribution of the *Lepidoptera* indicates that the separation of Greenland from the European land-mass took place at a much more ancient date. But Iceland and the Faroes may have been still sufficiently close to the British Isles to be connected to them by land during the early part of the Upper Pleistocene glaciation. The fact that

there are in Iceland and the Faroes certain species of Lepidoptera which probably spread over the British Isles after the maximum of the first glacial phase would indicate that this land-connection was in existence until early in the first interstadial phase.

It may be concluded, therefore, that *X. exulis* dates from the first glacial phase as an inhabitant of Scotland and the Shetlands. That it must be a relatively ancient inhabitant of those regions is also indicated by its variation: it is represented there by the apparently endemic ssp. *assimilis* Doubleday.

Eulype subhastata Nolcken may have arrived in the same way at the same time. It is an inhabitant of the subarctic regions of Europe, Asia, America and Iceland and has its headquarters in the British Isles in the Hebrides, occurring also in the Scottish Highlands and doubtfully in the Shetlands (fig. 4).

(d) The Alpine Species.

There are six species which probably spread into the British Isles from the Alpine region during the first glacial phase. Their distributions in the British Isles indicate that they all have had the same history. With the exception of *P. captiuncula*, they are found locally in the northern mountains of Great Britain and in the mountains of western Ireland.

An Alpine origin is well indicated in the case of *Erebia epiphron* Knoch, as on the Continent the species is found only in the mountains of central Europe. The antiquity indicated by its discontinuous distribution in the British Isles (fig. 5) is further indicated by its variation. It is represented in the Lake District of north-west England by the ssp. *mnemon* Haworth form *mnemon*, in the Scottish Highlands by the ssp. *mnemon* form *scotica* Cooke and in Ireland (Sligo and Mayo) by the ssp. *aetherius* Esper form *nelamus* Boisduval. Its distribution and variation indicates that after it first spread over the British Isles it had its range divided. One population became isolated on the now-submerged land west of Ireland and the other probably in England, south of the ice-sheets which were responsible for the division of its range. The ice-sheets of the second glacial phase must have been responsible for this; those of the third were not sufficiently extensive in Ireland to restrict the species to the western glacial land. Thus the species probably spread over the British Isles during the first glacial phase—for reasons discussed below, probably at a late stage of that phase. The forms *scotica* and *mnemon* probably developed as a result of a similar division of the species' range in Great Britain during the third glacial phase: as the ice of the second glacial phase retreated the species spread northwards in Great Britain and later had its range there divided by the advance of the Highland ice of the third glacial phase and the two populations so produced then developed independently of each other.

The Alpine origin of *Apatele euphorbiae* Fabricius is indicated by its being represented in the British Isles by a subspecies, *myricae* Guenée, which is very similar to the Alpine ssp. *montivaga* Guenée. It probably

has had a similar history to the last species. In central Scotland it is found only on the mountain moors, but in Aberdeen and Kincardine it is found only on the lowlands in the coastal districts, according to Horne (1890) and Reid (1891). This probably resulted from the effects of the third glacial phase: the species' range in Scotland was divided by the advance of the ice, one population surviving on the ice-free land along the east coast from which it did not spread in postglacial times and the other surviving on the more extensive land west of the ice-sheets.



FIGS. 4-9.—Types of ranges of first glacial phase Lepidoptera.

Gnophos obfuscaria Schiffermüller is another species whose probable Alpine origin is indicated by its variation. The typical subspecies, found in the British Isles, apparently also is the subspecies found in the Alpine region, the fuscous-grey ssp. *myrtillata* Thunberg occurring in northern Europe. The species' distribution in the British Isles indicates that it too was an inhabitant of the now-submerged glacial land west of Scotland and of Ireland during the second glacial phase. It is found in the mountains of Scotland and of western Ireland.

In the case of the remaining three species definite evidence of an Alpine origin is lacking at present. However, as they have ranges and

distributions in the British Isles which are similar to those of the species discussed above and differ in type from those of the northern European species discussed in section (e) it seems likely that they did spread into Britain from the Alpine region.

Phothedes captiuncula Treitschke has been found in northern England, in the Burren district of western Ireland and, according to Professor J. W. Heslop Harrison (*in litt.*), in the Isle of Rhum (fig. 6). Its present distribution in Great Britain can be explained by assuming that the population which survived in England south of the ice-fronts, when the ice of the second glacial phase divided the species' range, did not spread northwards when the ice retreated, as did that of, for example, *E. epiphron*. The Irish and the Hebridean colonies are the survivors of the population which inhabited the western glacial land during the second glacial phase. That they have been long separated from the English population is indicated by taxonomic evidence: the species is represented in England by the ssp. *expolita* Stainton which is found abroad only in south Denmark (see p. 304), and is represented in Ireland (and ? in Rhum) by the ssp. *tincta* Kane.

The variation of *Entephria flavicinctata* Hübner indicates that its Scottish population probably represents one which survived the second glacial phase on the land west of that country, while the northern Irish and northern English populations represent one which survived south of the ice-fronts: the species apparently is represented by the ssp. *ruficinctaria* Guenée in Scotland and by a grey race in England and Ireland.

Dysstroma concinnata Stephens, whose distribution probably has not been fully worked out, may have survived the second glacial phase only on the glacial land to the west, and not to the south of the ice-fronts in England. It has been found in the Scottish Highlands, the Hebrides and the mountains of western Ireland. It is represented by a distinct subspecies, *oressigena*, in Ireland. Like the other species, it probably was a first glacial phase arrival.

The distributions of these Alpine species in the British Isles would indicate that they have had somewhat different histories from the northern European species to be discussed next. One point is that they survived the second glacial phase on the land west of Ireland while the northern European species did not. There is evidence that both groups of species arrived during the first glacial phase, but it is not unlikely that they arrived at different times during that phase. There was a change from more oceanic to more continental climates during the course of each glacial phase, with a consequent replacement of tundra and subarctic vegetation by steppe vegetation in the regions immediately south of the ice-fronts. Possibly the northern European species arrived during the early part of the first glacial phase while the Alpine species arrived when steppe conditions prevailed. Some supporting evidence is provided by the fact that the distributions of these Alpine species indicate that they may have had subsequent histories very similar to some of the first interstadial arrivals discussed in the next chapter—the species which probably spread into the British Isles from the Pyrenean region.

Furthermore most of them inhabit mountain grasslands while the northern European species inhabit heaths and moorlands. It is not clear, however, why the Alpine species should have survived the second glacial phase on the land west of Ireland while the northern European species apparently did not. Studies of their ecology might throw some light on this point.

(e) *The Northern European Species.*

Next there is a number of species which have Boreo-Alpine distributions abroad—they occur in northern Europe and in the mountains of Central Europe, but not in the intervening areas—and in the British Isles they are confined to the mountains of the north (figs. 7 and 8), several of them occurring only at high elevations. Their habitats and distributions indicate that they date from a cold period and that they are amongst the most ancient of the cold period arrivals. A northern European origin is indicated by the variation of *Carsia sororiata* Hübner (*paludata* Thunberg nec L.) which is represented in the British Isles by its northern European subspecies, *imbutata* Hübner. Several other species are represented in Britain by endemic subspecies—an indication that they are ancient inhabitants. They include *Amathes hyperborea* Zetterstedt (*alpicola* Zetterstedt) ssp. *alpina* Humphreys and Westwood, *Perizoma minorata* Treitschke ssp. *ericetata* Stephens and a race of *Poecilopsis lapponaria* Boisduval. These species, together with *Triphaena sobrina* Guenée, *Anarta cordigera* Thunberg, *A. melanopa* Thunberg, *Coenocalpe lapidata* Hübner, *Isturgia carbonaria* Clerck and *Psodos coracina* Esper (*trepidaria* Treitschke nec Hübner) probably date from the first glacial phase as inhabitants of the British Isles. Like other first glacial phase arrivals with the exception of *X. exulis*, they probably spread into southern England from north-central Europe. It is likely that this took place during the maximum of the first glacial phase, before the arrival of the Alpine species. That they did spread from north-central Europe is indicated by the survival of *A. cordigera* and *C. sororiata*, as well as of *P. captiuncula*, which also has a Boreo-Alpine type of distribution, in Denmark, the region from which they spread into Britain. As the ice-sheets retreated these species moved northwards in their wake, eventually becoming extinct in the southern parts of the British Isles when the climate became unfavourably warm there during the second interstadial phase. During that phase they probably became confined to the Scottish mountains, the only situations where suitable ecological conditions still existed. On the advance of the ice of the second glacial phase the species were forced southwards and westwards, returning to the Scottish mountains once more during the second interstadial phase. The same probably occurred during the third glacial phase and in early postglacial times.

Of the species under discussion only *C. sororiata* and *C. lapidata* occur in Ireland, where each is confined in the northern half of the country. Their Irish histories are not clear. Possibly they have survived since the last (third) glacial phase. More probably, however, they spread

into Ireland from Scotland in early postglacial times (see p. 356). If this was so then it is apparent that all these species must have become extinct in Ireland at some time in the past; possible causes of these supposed extinctions are discussed on pp. 325-6.

An additional species which may have had a northern European origin and may date from the first glacial phase is *Amathes ashworthii* Doubleday, found in the British Isles only at considerable elevations in the mountains of north Wales (fig. 9). Its antiquity as an inhabitant of that region is indicated by its being represented there by the endemictypical subspecies, that found on the Continent being the ssp. *candelarum* Staudinger, although a form very similar to *ashworthii* has been found in Scandinavia. The history of this species is difficult to reconstruct. Possibly it survived the later glacial phases on the unglaciated summits of the highest mountains of north Wales which projected above the ice-sheets.

(f) Other First Glacial Phase Arrivals.

Turning to the species which have wider ranges in the British Isles than those discussed above, the four juniper-feeding species may be dealt with first. They have discontinuous distributions in the British Isles, the distributions being regulated by occurrence of their food-plant as a native. They occur in Great Britain mainly on the chalk downs of southern England, in north Wales and in the Scottish Highlands. In Ireland *Eupithecia sobrinata* Hübner has a wide distribution over the northern half of the country, *Thera cognata* Thunberg (*simulata* Hübner *coniferata* Curtis) occurs locally in the west and *Eupithecia intricata* Zetterstedt has been taken in Kerry. The fourth species, *Thera juniperata* L. has not been found in Ireland. Incidentally, *E. sobrinata* is more widely distributed in the British Isles than the others. This almost certainly is due to the species' preference for the cultivated forms of juniper which has led to its artificial introduction into many localities in which it did not occur as a native.

That these species must have invaded the British Isles during a relatively cold period is indicated by their ranges abroad: *T. cognata* has a Boreo-Alpine distribution, while the others are found in northern and central Europe. It is also indicated by their food-plant, which probably grew in the sub-arctic zone south of the ice-fronts.

The antiquity indicated by the species' discontinuous distributions in the British Isles is confirmed by their variation, which is such as to indicate that the English populations have been isolated from the Irish and Scottish for a relatively very long period of time. *T. cognata* is represented by a richly-coloured form in Scotland and Ireland, *T. juniperata* by the ssp. *scotica* Staudinger in Scotland, *E. sobrinata* by the ssp. *anglicata* Herrich-Schäffer in England and by the ssp. *scotica* Dietze in Scotland (and ? Ireland), and *E. intricata* by the ssp. *arceuthata* Freyer in England (and ? Ireland) and by the ssp. *helveticaria* Boisduval in Scotland.

These species probably date from the first glacial phase as inhabitants

of the British Isles, and perhaps arrived at a stage in the retreat of the ice rather than during its advance or at its maximum. Their distributions and variation indicate their considerable antiquity. That *E. sobrinata*, at least, is as ancient an inhabitant of the British Isles as *X. exulis* is indicated by its occurrence in Iceland, where it is represented by an endemic subspecies. The four species probably spread over the British Isles as the ice-sheets of the first glacial phase retreated. Later, their ranges were divided by the advance of the ice of the second glacial phase, one population of each inhabiting England south of the ice-fronts and the other the now-submerged glacial land west of Scotland and of Ireland. During their isolation from each other the two populations developed independently. The glacial land populations spread eastwards into Scotland during the second interstadial phase and were later forced on to the glacial land once more by the ice of the third glacial phase. A population of *E. intricata*, however, was isolated in eastern Scotland by that ice and developed independently into the race *anglicata* Mill, which is now found in the Pentland Hills. In early postglacial times they spread eastwards once more from the glacial land into Scotland and western Ireland.

There is a possibility that while the Scottish and Irish populations of these species date from the first glacial phase the English populations may represent later invasions of the British Isles. But in view of the local distributions of the English races, and the high degree of endemic variation they exhibit, this seems less likely than the theory that the species are wholly of first glacial age as inhabitants of the British Isles.

Another species which probably dates from the first glacial phase is *Perizoma taeniata* Stephens. It has a Boreo-Alpine distribution on the Continent and this, together with its distribution and variation in the British Isles, may indicate that it has had a history similar to the juniper-feeding species. It is found locally in south-western England, north Wales, northern England, the Scottish Highlands and northern and south-western Ireland. The brownish-coloured form found in England probably represents a population which survived south of the ice-fronts of the second glacial phase, while the yellowish Scottish and reddish-yellow Irish forms represent the population which survived on the western glacial land.

Only of the species discussed above is there reasonably good evidence to indicate that they date wholly from the first glacial phase as inhabitants of the British Isles. Many of the species discussed in Chapter VII also may date wholly from that time, but definite evidence of this is lacking. Most of the glacial-phase arrivals probably invaded the British Isles during the first glacial phase and again during the second and third. In most cases it is impossible to say which of them may have arrived during the first, as the later arrivals have obliterated all trace of the earlier survivors. However, the non-migratory species which are found in Iceland may date originally from the first glacial phase as inhabitants of the British Isles. They include the Boreo-Alpine *Xanthorhoë munitata* Hübner and *Entephria caesiata* Schiffermüller, and *Characaeae graminis* L. and *Plusia interrogationis* L., all of which have

northerly distributions in the British Isles, the heath races of *Diarsia festiva* Schiffermüller (*primulae* Esper), *Ceramica pisi* L., *Hydriomena furcata* Thunberg (*sordidata* Fab., *elutata* Hübner) and *Eupithecia satyrata* Hübner, and *Xanthorhoë designata* Hufnagel, *Dysstroma citrata* L. (*immanata* Haworth) and *Epirrhoë alternata* Müller. The subsequent histories of these species will be discussed in greater detail later.

VI. THE ARRIVALS OF THE FIRST INTERSTADIAL PHASE OF THE UPPER PLEISTOCENE.⁴

The first interstadial phase of the Upper Pleistocene glaciation apparently was at least as long as the time which has elapsed between the end of the Ice Age and the present day; Movius (1942) suggests that it may have been of interglacial magnitude. The ice had disappeared completely from the British Isles, or at the most existed only locally in the western Highlands of Scotland. Deciduous forest covered most of England and the plant and animal remains indicate that the climate was no more severe than that of the present day, and in fact may have been rather warmer than now. In Scotland, pine and later birch were the dominant trees, but small amounts of other trees also occurred (Movius, 1942).

It is reasonable to conclude that during this long temperate period the British Isles supported a lepidopterous fauna which was at least as rich in species as that of the present day. As large areas of land in the region of the British Isles were not ice-covered during the subsequent glacial phase many of these species could have survived. These are the species discussed in this chapter.

It is usually easier to reconstruct the histories of Lepidoptera which arrived during the relatively temperate periods than of those which arrived during the glacial phases. This is because the latter were forced to change their headquarters on more than one occasion by the climatic and vegetational changes which accompanied the advances and retreats of subsequent ice-sheets, with the result that zoogeographical evidence often is of comparatively little value in the reconstructions of their histories. But the majority of the interstadial arrivals did not move from one region to another and back again as the ice-sheets expanded and contracted. For some reason they did not tend to recolonise a region from which they had been driven when ecological conditions there became favourable to them once more. Because of this it is often possible to date the times of their arrivals more confidently than with the glacial phase arrivals: the extent and position of their present ranges compared with the extent and position of past ice-sheets often provide an indication of which ice-sheet was responsible for the restriction of their ranges, so that the time of their arrival may be placed at not later than the preceding interstadial phase.

⁴ This is the Second inter-glacial period of Stamp (1946), and apparently of Ford (1945) who, however, places it before the maximum glaciation. It is also known as the Aurignacian oscillation.



FIGS. 10-17.—Types of ranges of first interstadial phase Lepidoptera.

FIG. 18.—Directions of spread of the first interstadial survivors during and following the retreat of the last ice-sheets.

Most of the species which survived the second glacial phase did so by becoming confined to the parts of the ice-free regions where ecological conditions favourable to them still existed, but some survived by adapting themselves to the new conditions. These may be dealt with first.

(a) *The Maritime Species.*

The effect of the sea on the climate of the coastal districts is to raise the winter and lower the summer temperatures in comparison with inland localities having the same average annual temperatures. Because of the milder winter temperatures Lepidoptera characteristic of the sea-coasts could survive a glacial phase with less difficulty than species characteristic of inland habitats. Some inland species took advantage of the coastal climate and became confined to the coasts during the second glacial phase and did not return to their inland habitats when climatic and other ecological conditions inland became favourable once more in postglacial times.

The majority of these species are represented in the British Isles by apparently endemic subspecies—an indication that they are comparatively ancient inhabitants; others exhibit local variation in parts of the country. The majority are confined to or have their headquarters on the southern and western coasts. The species are as follows:

- Eilema caniola* Hübner: S. England, S. Wales, Isle of Man, Dublin and Waterford (fig. 14).
Setina irrorella Clerck: S. England, Isle of Man, Scotland, Hebrides, Burren district (race *flavicans* Boisduval).
Cryphia muralis Förster (*glandifera* Schiffermüller): Cambridge (race *impar* Warren), S. and S.W. England, Wales, S. and W. Ireland (local forms).
Luperina nickerlii Frey ssp. *incerta* Tutt: N. Wales and Lancashire.
Nonagria sparganii Esper: S. and S.E. England, Cork.
Agrotis trux Hübner ssp. *lunigera* Stephens: S. and S.W. England, Wales, E. Scotland, E. and S. Ireland.
Aporophyla australis Boisduval ssp. *pascuea* Curtis: S. and S.E. England, S. and S.E. Ireland (fig. 15).
Cucullia absinthii L.: S.W. England, Wales, Cork.
Antitype xanthomista Hübner ssp. *nigrocincta* Treitschke: S.W. England, S. Wales, Isle of Man.
Hadena caesia Schiffermüller ssp. *manani* Gregson: Isle of Man, S. and W. Ireland (fig. 11).
H. andalusica Staudinger ssp. *barrettii* Doubleday: S.W. England, Wales, E. and S. Ireland (fig. 12).
Heliophobus albicolon Hübner ssp. *cinerascens* Tutt: Very local around coasts of British Isles.
Sterrhia rusticata Schiffermüller ssp. *vulpinaria* Herrich-Schäffer: S. and S.E. England, St. Kilda (fig. 16).

S. ochrata Scopoli ssp. *cantiata* Prout : S. and S.E. England.

Nyssia zonaria Schiffermüller : Hebrides (race *atlantica* Harrison), N. and W. Ireland (whitish race), N. Wales, Cheshire and Lancashire (fig. 10).

Zygaena achilleae Esper ssp. *caledonica* Reiss : Inner Hebrides, Oban district.

Z. purpuralis Brünnich (*pilosellae* Esper) : Hebrides and Oban district (ssp. *caledonensis* Reiss), Burren district (ssp. *hibernica* Reiss), N.W. Wales.

The taxonomic and zoogeographical evidence indicates that these species are amongst the most ancient of the lepidopterous inhabitants of the British Isles. The fact that some are confined to and others have their headquarters on the south-western and western coasts, where the winter temperatures are the mildest of any part of the British Isles at the present day, indicates that they arrived in and spread over the country at a time when the climate was at least as warm as now. There are indications that it may have been rather warmer than now : *A. australis* is a southern European species and the majority of the remainder have southern and central European ranges. There are also indications that dry and sunny conditions prevailed at the time of their spread over the country : *N. zonaria*, *Z. achilleae* and *Z. purpuralis* are day-flying and sun-loving species which frequent relatively dry situations in the British Isles, the first species occurring on sandhills and sandy pastures, the second on dry, sheltered banks and the third on limestone hillsides. As will be shown below, the species' distributions indicate that they inhabited the now-submerged glacial coast-lines and thus were not postglacial arrivals. The majority are too widely distributed to have survived the maximum of the first glacial phase. Consequently it is safe to conclude that they date from the first interstadial phase, which was the longest, warmest and driest period between the first glacial phase and the end of the Ice Age.

Further evidence that they were first interstadial arrivals is provided by analogy with certain species which are represented by two sub-species in the British Isles, namely :

Eumichtis lichenea Hübner : Grey race on E. and S. coasts of England ; green race on coasts of S.W. England, Wales, W. Scotland, E., S. and W. Ireland.

Hadena lepida Esper (*carpophaga* Borkhausen) : ssp. *lepida* in England, Wales and S. Scotland ; ssp. *capsophila* Duponchel in Ireland and Isle of Man.

Eupithecia denotata Hübner (*campanulata* Herrich-Schäffer) : ssp. *denotata* on chalk downs of S. and E. England ; ssp. *jasionecta* Crewe on coasts in S.W. England, N. Wales and S.W. Ireland (fig. 17).

Their variation indicates that each of these species invaded the British Isles on two occasions, separated from each other by a long period during which no invasions took place. The distributions of the typical subspecies are such as to indicate that they were postglacial arrivals (see p. 349); they reached England over the southern part of the North Sea, when that region was dry land in the early postglacial, and then spread northwards and westwards. The distributions and the degree of variation of the second subspecies of each of the three indicate that these subspecies were earlier arrivals and that they have had histories as British species similar to the maritime species listed above.

Although all the species listed above are wholly or mainly maritime in their habits in the British Isles, none appears to be exclusively or characteristically maritime on the Continent. Some, in fact, are characteristic of types of country very different from their British habitats. For instance, *A. trux*, *H. caesia*, *H. andalusica* and *H. lepida* ssp. *capso-phila* are characteristically mountain species abroad, *E. caniola*, *S. ochrata*, *Z. purpuralis* and *Z. achilleae* occur on the mountains as well as on the lowlands, while *N. zonaria* is found in damp meadows and wooded country and *H. albicolon* in open grasslands. It is reasonable to conclude that when they first spread over the British Isles they inhabited situations ecologically similar to those which they still inhabit on the Continent. The climatic deterioration which accompanied the advance of the ice-sheets of the second glacial phase probably exterminated them in their inland habitats. Only on the coasts, particularly the south-western and western coasts, did favourable climatic conditions still exist because there the proximity of the ocean raised the winter temperatures. In order to survive that glacial phase the species were forced to adapt themselves for life on the coasts. Once having done so they did not revert to their original habits when conditions inland became favourable once more in postglacial times. *E. denotata* was forced to change its food-plant as well as its habitat. Its typical subspecies feeds on *Campanula trachelium* and this plant probably was exterminated, so that the first interstadial population had to find alternative food and selected *Jasione montana*, on which that population (now represented by *jasioneata*) still feeds. Chapman (1899) suggests that the way in which the mild winter temperatures affect certain of the species is that they permit the larvae to emerge and feed during dry spells, thus enabling the species to complete their life-cycles in a year, which might be impossible if the winters were colder. *A. australis* and *E. caniola* probably are affected in this way.

Most of the species probably spread into the British Isles during the first interstadial phase from the lowlands of central Europe, but there are some which probably arrived from the Pyrenean region, namely, *A. trux*, *H. andalusica* and *H. caesia*, species which inhabit the mountains of Spain and southern France. It is known that the Pyrenees were glaciated during the Ice Age and the presence of the ice there may have forced the species on to the lowlands of France whence they spread into the British Isles. Thus they may have arrived before the ice of the first glacial phase had disappeared and, judging from their distributions in the

British Isles, it is not unlikely that they arrived at about the same time as the Alpine species discussed in the last chapter. Probably these mountain species, and also the remaining British maritime species listed above, invaded the British Isles at the time in the retreat of the ice of the first glacial phase when steppe conditions prevailed and the climate was relatively continental. On their distribution and variation it is difficult to draw any definite line of distinction between them and the Alpine species. For example the distribution of the Alpine *G. obfuscaria* is very similar to that of *N. zonaria* and certain of the British races of *Z. purpuralis* and *Z. achilleae* are said to resemble Alpine races more closely than they resemble races of the species from any other parts of Europe.

The distributions of the species in the British Isles enable their histories to be reconstructed in some detail. As explained above, they probably spread over the British Isles during the first interstadial and became confined to the coasts during the second glacial phase. It must be borne in mind that owing to the great eustatic lowering of the sea-level the coast-lines at that time were far west and south of their present situations. As the sea-level rose in late-glacial and early postglacial times the coast-line receded eastwards and, south of the British Isles, north-eastwards, so that the species did not come to inhabit most of their present localities until the sea had reached approximately its present level in the postglacial (fig. 18). The present distribution of *Z. achilleae* indicates that it survived from the second glacial phase to the early postglacial mainly on those parts of the glacial coast-line west of what is now Scotland. *N. zonaria* and *Z. purpuralis* survived mainly in the same region but also on the coasts west of Ireland. The remaining species survived on the glacial coast-lines south-west of England and of Ireland, *S. irrorella*, *H. albicolon*, *E. lichenea* and *S. rusticata* also surviving on the coasts west of Scotland.

At the time of the low sea-level it seems probable that a broad river, composed of drainage from the land and from the ice-fronts, flowed southwards over the low-lying region now occupied by the Irish Sea and St. George's Channel. This may explain why such species as *L. nickerlii*, *A. xanthomista* and *S. ochrata* apparently do not occur in Ireland: they may have arrived in England too late in the first interstadial to be able to reach Ireland—the sea-level had become high enough to isolate that country—and during the second glacial phase inhabited the coast-line south and east of the estuary of this river, the estuary forming a barrier which effectively prevented them from spreading on to the coasts of the Irish land-mass at a later date.

A southerly and easterly type of distribution in Ireland is unusual amongst Lepidoptera but several of the species under discussion have been found only or mainly in the south-east or south and east of that country, *E. caniola*, *A. trux*, *H. albicolon*, *H. andalusica* and *A. australis* being examples. Their south-easterly Irish and south-westerly British distributions can be explained by assuming that the species came to inhabit both the east and the west coasts of the great bay which must

have been formed when the gradually rising sea invaded from the south the low-lying region between Ireland and Great Britain (fig. 18).

The markedly discontinuous distributions in the British Isles of many of the above species which have relatively wide ranges probably is due to their having been exterminated on many parts of the former coast-line by the rising sea. This is particularly evident in the case of *S. rusticata*, which is now known to survive in the north only in St. Kilda, a small island more than forty miles west of the Outer Hebrides. It will be noted that the adults of the majority of the more widely-distributed species are large and relatively powerful in flight and thus could have accompanied the receding coast-lines more easily than could such feebly-flying species as *S. rusticata* or such relatively sedentary species as *N. zonaria* and *Z. purpuralis*.

N. zonaria, *Z. achilleae* and *Z. purpuralis* are not strictly confined to the coasts in western Scotland and the Hebrides, but also occur inland, sometimes at considerable elevations. This could be explained by the fact that during the third glacial phase the sea-level in that region was much higher than now in relation to the land because the isostatic sinking there of the land due to the great weight of the Highland ice-sheet. At that time the species must have inhabited the coastal districts and when the land later rose in relation to the sea they remained attached to the former coast-lines. The reason for this may have been that by then (*i.e.*, in the early postglacial) the climate had become temperate and there was therefore no necessity for the species to remain attached to the coasts. The occurrence of other species inland, for example of *S. irrorella*, *C. muralis* and *A. trux* in the Cotswold and Mendip hills, probably was due to a similar cause. With these species, however, the Romano-British rise in sea-level, when the sea flooded the low-lying valleys between the ranges of the Cotswold and Mendips, may have been responsible. The occurrence of colonies of the lichen-feeding *C. muralis* inland in towns—in Cambridge and Cork—may be due to the buildings being suitable for the growth of its food-plants or to their producing sufficient warmth in winter to enable the species to survive inland.

There are several other maritime species which may have had histories similar to those discussed above, but the evidence is less clear and it is possible that some of them may have arrived during the post-glacial climatic optimum and have had their ranges or distributions restricted by the climatic deterioration of the later postglacial. Like the species discussed above, however, all are confined to the coasts in Britain and all apparently occur inland abroad. None has been found in Ireland. *Leucania putrescens* Hübner, *Ophiusa cracca* Schiffermüller, *Sterrrha degeneraria* Hübner and *Thymelicus acteon* Rottenberg, are confined to the south-western coasts of Great Britain, *Leucochlaena hispida* Geyer, *Caradrina ambigua* Schiffermüller, *Sterrrha humiliata* Hufnagel and *Melitaea cinxia* L. to the south coast and *Lasiocampa trifolii* Schiffermüller to the south coast and the coasts of Lancashire and Cheshire. As compared with that of the species previously discussed these species do not exhibit much racial variation. *S. humiliata* is said

to be represented in England by a race which is smaller and less bright, and *C. ambigua* by a race which is less ashy in colour, than the continental forms, while *L. hispidula* and *O. cracca* develop endemic local forms in parts of their ranges in England. The variation of *L. trifolii* might indicate that it invaded England on more than one occasion: the ordinary English race, *rufa* Tutt, may represent a first interstadial invasion while the race *flava* Tutt, which occurs on the coast of Kent and is said to have assembling and flight habits different from those of *rufa* (Kettlewell, 1937), may represent a postglacial invasion.

There are two species which are characteristic of the sea-coasts abroad as well as in Great Britain but whose distributions indicate that they may have had a history similar to the species discussed above: *Agrotis ripae* Hübner, found very locally on the coasts of Great Britain south of Yorkshire in the east and Ayrshire in the west, of the Isle of Man and of eastern and southern Ireland, and *Aegeria philanthiformis* Laspeyres (*muscaeformis* Vieweg nec Esper), occurring on the coasts of south-western England, Wales, eastern Scotland and southern Ireland (fig. 13). Their distributions are comparable with those of some of the species described above, for example with that of *A. trux*, and it seems likely that they too date from the first interstadial phase. The antiquity of *A. ripae* is further indicated by the local forms the species has developed in different parts of its range in the British Isles. Incidentally the occurrence of *A. trux* and *A. philanthiformis* on the eastern coasts of Scotland can be explained by assuming that they spread into that region during the second interstadial phase and survived there through the third glacial phase, when the ice-sheets did not cover the east coast.

There are two other maritime species whose variation indicate possible first interstadial origins: *Agrotis cinerea* Hübner and *Euxoa tritici* L. The latter is widely distributed around the coasts of the British Isles, the former occurs very locally in England and Wales, in Perthshire and in east Tyrone. Each is represented by two subspecies in the British Isles, one occurring mainly on the coasts and the other mainly inland in southern England. It is possible that the two races of each species represent distinct invasions. If so, the inland races, *A. cinerea* ssp. *tephrina* Staudinger and *E. tritici* ssp. near *aquilina* Schiffermüller, represent the earlier invasions as they appear to exhibit a greater degree of endemic variation than do the maritime races. A more likely explanation of the species' histories is as follows: they first spread around the coasts of the British Isles and into ecologically suitable localities inland at a time of relatively high sea-level—perhaps during the part of the first interstadial when the sea-level was similar to or rather higher than that of the present day. As the sea-level fell later, the inhabitants of the coasts moved further and further away from the inhabitants of the inland situations and eventually the two populations of each species became isolated from each other by long distances and by belts of country in which ecological conditions were unfavourable—perhaps by belts of woodland. During their isolation the two populations were able to develop independently of each other. The inland

populations developed a greater degree of endemic variation because of the relatively smaller number of individuals involved and because they must have been affected by climatic changes to a much greater extent than were the inhabitants of the coasts, as the latter inhabited situations where the annual range of temperatures was reduced by the proximity of the sea. When the sea-level rose in late-glacial and early postglacial times the maritime populations were brought nearer to the inland populations once more.

The occurrence of *A. cinerea* in Ireland only in east Tyrone is not easy to explain. *E. tritici* ssp. ? *aquilina* has been reliably recorded from Ireland only from the same district. Possibly they spread into that region at the stage in the retreat of the second glacial phase ice when that region was not ice-covered although extensive ice-sheets covered northern Ireland further west. The two have been found in east Tyrone only on the moraines which mark a readvance (a major readvance, according to Movius, 1942) of the retreating ice-sheets of the second glacial phase.

The relatively wide distribution of *E. tritici* in comparison with that of *A. cinerea* probably is due to the former species' migratory habits, which allowed it to recolonise localities in which it had been exterminated during the glacial phases. The discontinuous distribution of *A. cinerea* indicates considerable antiquity.

(b) *The Marsh and Fen Species.*

Next to be discussed are species which are confined to fens or marshes in the British Isles but in most cases frequent other types of habitat abroad. With them may be included a few species which are maritime in their habits in the British Isles but not abroad and whose maritime habits probably are due to a cause different from that which affected the species discussed in the last section.

Most of these species are confined to south-eastern England and have their histories indicated mainly by taxonomic and ecological evidence, but there is one whose history is indicated also by zoogeographical evidence. This is *Eustrotia olivana* Schiffermüller (*bankiana* Fabricius, *argentula* Hübner), which occurs only in the East Anglian Fenlands and in south-western Ireland (fig. 19). Its markedly discontinuous distribution indicates that it is a relatively very ancient inhabitant of the British Isles and its occurrence in Ireland only in the south-west indicates that it was an inhabitant of the glacial land south or south-west of that country during one of the more intense glacial phases. That the discontinuity of its distribution is of long standing is indicated by the fact that the English and the Irish races differ from each other both taxonomically and in habits. The Irish race is small and bright in comparison with the English and is found from the lowland swamps up to 1,500 feet on the hills and flies readily. In England the species is confined to fens and is a relatively shy insect. It is a day-flying and sun-loving species which frequents dry slopes and banks on the Continent. This would indicate that it spread over

the British Isles at a time when the climate was relatively dry and sunny. Its present preference for damp localities in Britain may be the result of its having adapted itself for survival through a relatively damp period so that when dryer conditions reappeared it became confined to the damp localities. Most probably it was a first interstadial arrival.

There is evidence that populations of *Lycaena dispar* Haworth and *Eilema pygmaeola* Doubleday have been isolated in the Dogger Land region for a very long period of time. This evidence is provided by the present occurrence of endemic subspecies in what were the eastern and western terminations of that land. The same applies to *Phothedes captiuncula* Treitschke (p. 291) and *Caenophila subrosea* Stephens (p. 329). The Dogger Land is the name given to the southern part of the North Sea when that region was dry land.

L. dispar is represented by the ssp. *rutilus* Werneberg over most of its range in Europe. In the British Isles, where it was found only in the East Anglian Fenlands and is now extinct as a native (see p. 278), it was represented by its typical subspecies, while a race very similar to that subspecies, the ssp. *batauius* Oberthur, is found locally on the coasts of Holland. Similarly, *E. pygmaeola* (fig. 20) is represented by the subspecies *pallifrons* Zeller over most of its range in Europe, while its typical subspecies is found locally on the coasts of Denmark and of south-east England. British *pygmaeola* exhibit some differences from Danish, chiefly in size (Lempke, 1933). The subspecies *dispar* and *pygmaeola* must have developed as a result of the isolation of populations of the species in the Dogger Land region for a long period of time. The differences between the eastern English and the western European representatives of the Dogger Land subspecies must have developed since those subspecies were exterminated except at the extreme easterly and westerly limits of their ranges by the postglacial submergence of the Dogger Land. As they differ from each other to a much lesser degree than either differs from the ordinary European subspecies it is apparent that the Dogger Land populations must have been isolated in that region for a far longer time than their surviving remnants have been isolated from each other. Consequently they must date from some time in the Pleistocene as inhabitants of that region.

Several other species which are found in the British Isles only in the East Anglian Fenlands are represented by distinct races there. These include *Papilio machaon* L. ssp. *britannicus* Seitz, the large, pale and strongly marked extinct British race of *Lymantria dispar* L. and *Euphyia polygrammata* Borkhausen ssp. *conjunctaria* Lederer. As British species these probably have had histories similar to the species just discussed. Incidentally the racial variation of *P. machaon* and *L. dispar* indicates that the effects of overseas migration have been negligible in these species in the past. Both are suspected migrants and also are artificially introduced from time to time.

Now the question arises as to why populations should have become isolated in the Dogger Land region at some time in the past. Past climatic changes provide a possible answer. During the first two

glacial phases of the Upper Pleistocene the climate of England and of the neighbouring parts of the Continent must have been cold because of the proximity of the ice-sheets. But as the Dogger Land was comparatively low-lying compared with those regions milder conditions may have prevailed there. The climate may have been sufficiently mild to permit the survival there of certain species of Lepidoptera which were exterminated by the cold on the relatively higher ground elsewhere in western Europe. It is unlikely that the ice-sheets of the third glacial phase could have caused such extirminations as they did not extend sufficiently far south in Great Britain. On the other hand, it is unlikely that the species could have survived the first glacial phase because then the ice apparently covered most of the Dogger Land. The ice-sheets of the second glacial phase, however, could have produced the requisite effects. This, together with the relatively high degree of endemic variation they exhibit, indicates that the species mentioned above probably date from the first interstadial phase as inhabitants of the region of the British Isles. Additional evidence is provided by analogy with *E. olivana*.

There are two species which have been found in the British Isles only in the coastal marshes of Kent and Essex: *Euchloris smaragdaria* Fabricius and *Malacosoma castrensis* L. (fig. 21). Evidence of their origin is best provided by analogy with *Leucania pallens* L. The typical subspecies of *L. pallens* is widely distributed over the British Isles in grassy situations and there is nothing to indicate that it was anything but a comparatively recent arrival. It may date from the postglacial but more probably dates from the second interstadial phase as it occurs in the Shetlands, islands which were not connected by land to Scotland in postglacial times. A second subspecies, *favicolor* Barrett, is found in the same localities and situations as *smaragdaria* and *castrensis* and has not been found elsewhere. It probably represents an earlier invasion of the British Isles by *L. pallens* than does the ssp. *pallens* and probably developed as a result of the isolation of a population of the species in the Dogger Land region for a long period of time. It is thus likely to have had a history similar to the species discussed above. Consequently it, *smaragdaria* and *castrensis* probably date from the first interstadial. *Eupithecia extensaria* Frey, found in coastal marshes in Norfolk and Yorkshire, may have had a similar history.

Many of the above species have different habitats in the British Isles from those abroad. The habitats of *E. olivana* have already been described. *E. pygmaeola* inhabits coastal sandhills, while *E. pallifrons*, of which it is probably a subspecies, is found in dry sandy woods, waste fields, etc., up to high altitudes in the mountains. *E. smaragdaria*, found only in salt-marshes in England, frequents the open parts of woods, dry ditches, etc., abroad. On the Continent it feeds on various small plants, while *Artemisia* and other salt-marsh plants are its chief food in England. *P. machaon* is found in England only in fens but on the Continent it inhabits open country from sea-level up to high altitudes in the Alpine pastures. Its sole food-plant in England is *Peucedanum palustre*, while abroad it feeds on various UMBELLIFERAE. Another fen species in England was *Lymantria dispar*, which inhabits woods and

forests abroad, being a serious woodland pest in some countries. Like *E. smaragdaria*, *M. castrensis* is found only in the coastal marshes in England, where it feeds on *Artemisia* and other plants, while on the Continent it inhabits open woods, heaths and open country generally and feeds on various small plants found in such situations. To these may be added *Apatele strigosa* Schiffermüller, whose distribution in the British Isles would indicate that it has had a similar history. It has been found only in the East Anglian Fenlands, while abroad it inhabits wooded country generally.

It will be noted that all these species with the exceptions of *A. strigosa* and *L. dispar* inhabit open country abroad. This provides a clue to a possible explanation for their changed habits in England. At the time when they first spread over the Dogger Land region ecologically suitable situations—situations ecologically similar to those which they now inhabit on the Continent—must have been widespread there. Thus the region cannot have been densely wooded. A later development of dense forests may have exterminated their food-plants except in situations where the trees could not grow densely. Consequently the species had to become confined to and adapted for life in those situations in order to survive. Some found the ecological conditions of the inland fens the most favourable and others those of the salt-marshes, while *E. pygmaeola* (at that time probably *pallifrons*) preferred the coastal sandhills. The food-plants of some of the species probably were completely exterminated by the supposed forest development so that those species were forced to attack whatever surviving plants proved palatable. Thus, *P. machaon* found *Peucedanum palustre* the most suitable alternative to its usual food-plants and as a result became confined to the fens where this plant grows in abundance, while *E. smaragdaria* and *M. castrensis* (and ? *E. extensaria*) took to *Artemisia maritima* and other salt-marsh plants and consequently became confined to the coastal marshes.

Although *L. dispar* and *A. strigosa* are woodland species abroad it is possible to apply this explanation to them also. The latter species feeds on hawthorn, a shrub which does not grow in dense forests but, under natural conditions, is characteristic of the margins and glades of woodlands. Thus a development of dense forests would have the effect of confining it to the fen margins. Evidence that this did in fact take place is provided by the species being an inhabitant of the margins and "islands" of the Fenlands at the present day. The forest development could have affected *L. dispar* provided that the dominant tree was one on which the species does not normally feed. It attacks many kinds of deciduous trees but apparently does not normally feed on conifers. Thus a development of pine forests may have been responsible for its restriction to the fens. For other reasons pine is likely to have been the dominant tree in this supposed forest development. It casts a deep shade and consequently small plants, including those which were the original food of the species which have changed their food-plants, are usually absent from dense pine forests. And during the second glacial phase the ice-sheets were sufficiently near the Dogger Land for

that region to be in the pine forest zone. During the course of each glacial phase there was a change from more oceanic to more continental conditions (Zeuner, 1945). Probably this supposed pine forest development took place towards the end of the glacial phase, when the more continental climatic conditions prevailed.

On zoogeographical and ecological evidence *Thymelicus lineola* Ochsenheimer and *Scopula emutaria* Hübner may have had histories similar to the above species. Both are found mainly in coastal marshes in England, but also occur less frequently in marshy situations inland, while they inhabit open country on the Continent, the former species being found at altitudes of up to 7,000 feet. However, unlike the species discussed above, they probably survived the second glacial phase in the region of the English Channel as well as in the Dogger Land, as they now occur in coastal regions in the south, as well as in the east, of England. *T. lineola* may have survived also in the region of St. George's Channel, whence its Somerset colony may have originated. Incidentally its distribution in south-east England provides a connecting-link between the Fenland species and the east coast salt-marsh species as it occurs in both situations. The antiquity of *S. emutaria* as an inhabitant of England is further indicated by taxonomic evidence: it is represented in the coastal districts by the race *subroseata* Haworth, while a grey race is found in some inland localities.

The climatic deterioration which isolated populations in the Dogger Land region must have exterminated the species over most of west-central Europe. With the later return of more temperate conditions the species spread westwards and recolonised that area. With the exception of *L. pallens* none of them spread into the British Isles. There is one species, however, which may date from the first interstadial phase, but which did not recolonise western Europe after its extermination there except in the Dogger Land region. This is *Arenostola brevilinea* Fenn, which has been found only in the Norfolk Broads and in Belgium—these colonies being the survivors of the Dogger Land population—and in the Caucasus.

As mentioned above, the postglacial submergence of the Dogger Land resulted in the extermination of most of the Dogger Land races except at the extreme easterly and westerly limits of their ranges. This applied mainly to the inhabitants of the inland localities; many of the inhabitants of the coast were affected rather differently. When the postglacial Dogger Land was in existence the rivers of eastern England and of western Europe flowed over it to reach the sea at its northern coast. At that time, therefore, the Dogger Land races of species like *E. smaragdaria*, *M. castrensis*, *L. pallens*, and *T. lineola* must have inhabited the marshes along the northern coast. As the sea-level rose that coast receded southwards until, some 7,500 years ago, the coast-lines had come to approximate roughly with those of the present day, so that it was not until that time that the species reached their present localities in England. Strictly speaking, therefore, the Dogger Land races of these species may not have become established in what is now England until postglacial times. *E. pygmaeola* and *E. extensaria* probably did not

accompany the receding coast-lines as did those species but, like the inhabitants of the inland fens, were exterminated except at the limits of their ranges. The present distribution of *E. pygmaeola* (fig. 20) indicates that it inhabited both the northern and the southern coasts of the postglacial Dogger Land, while that of *E. extensaria* indicates that it was an inhabitant of the northern coast only.

It may be mentioned that the draining of the Fenlands has greatly affected the ranges and distributions of the Fenland species. The reclamation of the Fenlands was commenced in Roman, or perhaps in pre-Roman, times but was not carried out extensively until the seventeenth century. Numerous extinctions of Lepidoptera must have taken place, but only those which resulted from the nineteenth century reclamations are on record. The reclamation of several extensive fens in the middle of that century, notably of Whittlesea Mere in 1851 and of Burwell Fen about 1860, was followed by the extinction of *Caenophila subrosea* (see p. 329), *Lycaena dispar* and *Lymantria dispar* as native species, while *E. polygrammata* and *Laelia coenosa* (see p. 347) gradually became scarcer, to become extinct some twenty years later.

Scopula marginepunctata Goeze is a species whose habitats and distribution indicate that it may have had a similar history to the species discussed above. It occurs around the coasts of Ireland, England, Wales, and south-west Scotland. The fact that it is more frequent in Ireland and in the western districts of Great Britain than in the east would indicate that it was an inhabitant of the now-submerged glacial land west and south of the British Isles. On the Continent it inhabits open country generally, but in the British Isles it is confined to the coasts and to a few localities, chiefly heaths, inland in coastal counties. These habits may be attributed to the same forest development which affected the other species, and the coasts and heaths must have been amongst the few types of country which were not densely tree-covered. Most probably this species dates from the first interstadial phase.

One other species may be included in this section: *Itama brunneata* Thunberg (*fulvaria* de Villers). It is represented by two races in Britain, one occurring in the East Anglian Fenlands and apparently feeding on *Salix* and the other in the native pine forests of the Scottish Highlands and feeding on bilberry (and ? pine). The latter apparently is the race found abroad. The distribution and habits of the Fenland race indicate that it may have had a history similar to the Fenland species described above and thus probably dates from first interstadial times. The Highland race may represent the same invasion but is the surviving remnant of a population which existed with unchanged habits through the second glacial phase on the glacial land west of Scotland. It is difficult to explain why the Dogger Land population, whose survivors are the Fenland race, should have changed its habits as it is obvious that the suggested development of pine forest which affected the other inhabitants of the Dogger Land would not have affected it.

Pine was the dominant tree in Scotland during part of the first interstadial and the survival of *I. brunneata* there might indicate that this tree has survived in the British Isles since that time, existing

through the glacial phases on the glacial land west of Scotland. It now survives as a native tree in the British Isles mainly (?only) in the Scottish Highlands where it forms pure woods of the apparently endemic variety *scoticus* (Scots Pine). This variety may have developed as a result of the isolation of tracts of this tree for a long period on the western glacial land.

If *I. brunneata* is of first interstadial age, then the races or forms of several Lepidoptera which are found exclusively or mainly in the native Highland pine forests may also represent survivals from that period. They include *Thera obeliscata* race *scotica* Staudinger, the dark Scottish form of *T. firmata*, the yellowish or greyish Scottish race of *Ellopija prosapiaria*, and *Bupalus piniaria* race *flavicans* B.-White. Elsewhere in the British Isles these species have been established by artificial introductions (p. 278). Some of the Scottish varieties have been found locally in parts of southern England. According to Tansley (1939) it is possible that some of the pine in southern England is the remains of native pine woods and the occurrence of these races there might indicate their sites.

(c) *The Heath Species and Races.*

The third main group of first interstadial survivors includes the Lepidoptera which changed their habits and became adapted for life on the heaths and moors which must have covered large areas of the ice-free regions of west-central Europe during the second glacial phase.

Perhaps the best examples are *Cleora cinctaria* Schiffermüller and *Selidosema plumaria* Schiffermüller (*ericetaria* de Villers). Their distributions and habits on the Continent indicate that they must have spread over the British Isles at a time when the climate was at least as warm as that of the present day. Both now have southern and central European distributions and on the Continent *C. cinctaria* feeds mainly on *Hypericum* and *Artemisia*, and *S. plumaria* feeds on *Lotus*, *Vicia*, *Genista*, *Dorycnium* and *Rumex*. Furthermore their present distributions and variation in the British Isles (see below) indicate that they survived the second glacial phase. It may be concluded, therefore, that they probably date from the first interstadial phase as inhabitants of the British Isles. The two species have markedly discontinuous distributions in Great Britain, where they occur locally in southern England and in the Scottish Highlands, and have westerly distributions in Ireland, *C. cinctaria*, in fact, being confined to the west (fig. 22). The southern English populations probably represent those which survived the second glacial phase south of the ice-fronts, while the Irish and the Scottish populations survived on the glacial land to the west. Confirmatory evidence of this is provided by the species' variation, which is such as to indicate that the English populations have been isolated from the Irish and Scottish for a long period of time: Irish and Scottish *C. cinctaria* often tend to be large and brightly-coloured, while the Irish race of *S. plumaria* tends to be small and to have the central stripe of the wings obsolete.



FIGS. 19-27.—Types of ranges of first interstadial phase Lepidoptera.

At the present time both species have very different habits in the British Isles from abroad. In Britain both are characteristically heath species, *C. cinctaria* feeding on heath and birch and *S. plumaria* on heather. These habits can be explained by assuming, as is very probable, that the original food-plants of the species died out in the region of the British Isles as a result of the climatic deterioration which accompanied the advance of the ice-sheets of the second glacial phase, so that in order to survive there the species were forced to adapt themselves to the conditions which prevailed on the ice-free areas and to feed on whatever plants formed the most suitable alternatives to their usual food.

Epicnaptera ilicifolia L. seems to be a parallel case. On the Continent it feeds on *Salix* and birch. These must have been its food-plants when it first spread into the British Isles, where it has been found only in Staffordshire and south Yorkshire. It may have survived in those regions since first interstadial times. At present (if it is not now extinct) it apparently feeds only on bilberry in England. Probably the advance of the ice of the second glacial phase resulted in the extinction of *Salix* and birch in the northern Midlands so that in order to survive there the species was forced to adopt bilberry as its food-plant. That the species is a relatively ancient inhabitant is further indicated by its being represented in England by a local race (Barrett).

A possible additional example is *Brachionycha nubeculosa* Esper, but its distribution renders its history difficult to reconstruct. It has been found in the British Isles only in the central Highlands of Scotland, the Rannoch district of Perthshire being its best-known locality. This, taken alone, would indicate that it may have had a history similar to some of the Alpine or northern European species discussed in the last chapter. But the species' habits indicate that it spread into Scotland during a relatively temperate period and survived a subsequent colder period there. On the Continent, where it has a northern and central European distribution, it feeds on various trees, including elm, but in Scotland it feeds only on birch. Possibly it spread into Scotland during the first interstadial phase, when that country was wooded, and was forced to adopt birch as its sole food-plant when the other trees died out as a result of the climatic deterioration of the second glacial phase. Good evidence is provided by other first interstadial survivors that birch did survive on the ice-free glacial land west of Scotland during the second glacial phase (see p. 360), but there is no evidence for the survival of other deciduous trees.

Next there is a number of species each of which is represented by two races in the British Isles, one race of each representing a population which survived since first interstadial times by adapting itself for life among heath and moorland vegetation, the other representing a post-glacial invasion. The species in question, and their races, are as follows :—

Celaena leucostigma Hübner (*fibrosa* Hübner) : (1) ssp. *leucostigma* in marshes and fens, feeding on *Cladium*, *Iris*, etc. ; (2) ssp. *scotica* Cockayne on heaths, feeding apparently on *Molinia*.

- Diarsia festiva* Schiffermüller (*primulae* Esper) : (1) woodland race ; (2) moorland race (*pseudoconflua* Bytinski-Salz, *conflua* auctt.)
- Eupithecia absinthiata* Clerck (*minutata* Treitschke) : (1) ssp. *absinthiata* in open grassy country, feeding on *Artemisia*, *Achillea*, *Senecio*, etc. ; (2) ssp. *goossensiata* Mabille on heaths and moors, feeding on heather, heath, etc.
- Eupithecia satyrata* Hübner : (1) ssp. *satyrata* in open woods and waste ground nearby feeding on *Centaurea*, *Scabiosa*, etc. ; (2) ssp. *cal-lunaria* Doubleday on heaths and moors, feeding on heather.
- Lygris testata* L. : (1) reddish or yellowish race in marshes and damp woodlands, feeding on *Salix* and birch ; (2) purplish race on heaths and bogs, feeding on heather.
- Hydriomena furcata* Thunberg (*sordidata* Fabricius, *elutata* Hübner) : (1) *Salix*-feeding race in woods and marshes ; (2) smaller and more variable bilberry-feeding race on heaths and moors, emerges about a month earlier than the *Salix*-feeding race.
- Operophtera brumata* L. : (1) ssp. *brumata* in wooded country, feeding on various trees and shrubs ; (2) ssp. *myricaria* Cooke on heaths and moors, feeding on *Myrica*.
- Oporinia autumnata* Borkhausen : (1) ssp. *autumnata* in woods and alder plantations, feeding on birch and alder ; (2) ssp. *filigrammaria* Herrich-Schäffer on moors, feeding on heather, bilberry, etc.
- Ectropis bistortata* Goeze (*biundularia* Borkhausen) : (1) ssp. *bistortata*, double-brooded ; (2) ssp. *crepuscularia* Hübner, single-brooded.
- Lasiocampa quercus* L. : (1) ssp. *quercus* in woods, hedges, coasts, etc., feeding on hawthorn and blackthorn, one-year life-cycle ; (2) ssp. *callunae* Palmer on heaths and moors, feeding on heather, two-year life-cycle.
- Trichiura crataegi* L. : (1) ssp. *crataegi* in wooded districts, feeding on hawthorn and blackthorn, one-year life-cycle ; (2) ssp. *ariae* Hübner on moors at high altitudes, feeding on heather, two-year life-cycle.

It is possible that a similar type of variation is exhibited by *Orgyia antiqua* L., *Abraxas grossulariata* L. and *Pieris napi* L., but these are species which must have had their ranges and distributions greatly altered in comparatively recent times—the first two by artificial introductions, the third by immigration. Consequently their earlier histories are difficult to reconstruct.

In the case of every species listed above, with the possible exception of *T. crataegi*, the first race probably represents a postglacial invasion of the British Isles. They all have wide distributions on the neighbouring parts of the Continent and their distributions in the British Isles are such as to indicate that they spread into England over the postglacial Dogger Land and then spread northwards and westwards. The occurrence in Ireland of the races whose ranges in Great Britain extend into central Scotland and the absence from Ireland of those whose ranges do

not extend so far north further indicates a postglacial origin, as the only postglacial land-connection between the two countries extended between western Scotland and northern Ireland (see p. 355). Finally, in no case is any greater antiquity indicated by taxonomic or ecological evidence.

T. crataegi has been found in Ireland only in Derry and Kerry. If the typical subspecies is that found in Ireland, then its distribution there would indicate that it was an inhabitant of the glacial land west of that country, and therefore that it is of interstadial age as an inhabitant of the British Isles. But if the Irish race is *ariae*, then there is nothing to indicate that the ssp. *crataegi* was anything but a postglacial arrival in Great Britain. Until information on the identity of the Irish race becomes available it is inadvisable to attempt a reconstruction of the history of ssp. *crataegi* as an inhabitant of Britain.

In no case has the second, or heath, race of a species a distribution in the British Isles which would indicate a postglacial origin. With the apparent exception of *C. leucostigma* ssp. *scotica* they all apparently occur on the Continent, but are confined to northern Europe or to the Alpine region. The most probable history of these races was as follows: they spread over Europe, as the typical races, during a temperate phase. During the following glacial phase each had its range divided by the ice-sheets. One population survived in Europe south and east of the Alpine and Pyrenean ice while the other inhabited the region of west-central Europe between and west of the Alpine and Pyrenean ice in the south and the Scandinavian and British ice in the north. Because of the proximity of the ice-sheets, tundra and moorland vegetation must have covered much of that region. Consequently in order to survive there the west-central European populations had to adapt themselves to these conditions. Their original food-plants probably were exterminated so that they were forced to feed on heath and moorland plants in order to survive. In addition the colder climates caused some species to lengthen their life-cycles in that region. Those populations have retained their acquired habits to the present day. The populations which inhabited southern and eastern Europe survived with unchanged habits, as they had retreated to areas where favourable ecological conditions still existed. *Ortholitha scotica* may have developed from *O. mucronata* in the same way.

It seems most likely that the ice-sheets of the second glacial phase were responsible for the splitting of the species' ranges and the changes in habits of the northern populations. Thus these heath races probably date from the first interstadial phase as inhabitants of the British Isles. It is less probable that they date from the last interglacial, when the ice-sheets of the first glacial phase would have been responsible for their heath habits. The reason for this is that it is reasonable to assume that the southern and eastern European populations would have spread westwards during the first interstadial, and as there is evidence of only one invasion of the British Isles in early Upper Pleistocene times it may be concluded that it took place at that time.

During the second interstadial phase these heath races probably spread northwards into northern Europe and over the British Isles,

moving southwards once more on the advance of the third glacial phase ice. In the early postglacial they retreated mainly to northern Europe and the Alpine region and into the northern and western parts of the British Isles, largely because of the distribution of heaths and moorlands. At the same time the populations which inhabited southern and eastern Europe during the latter part of the Pleistocene commenced to spread northwards and westwards, eventually spreading over most of the British Isles. As they frequent different types of habitat from the heath races there has been little contact between the two races of most of the species.

Both races of *O. autumnata* have northerly distributions in Ireland. For reasons to be discussed later (p. 325) this may indicate that the species became wholly extinct in that country before the end of the Pleistocene. Both races then spread into Ireland from Scotland in postglacial times. The fact that *filigrammaria* has a wider range in Ireland than *autumnata* supports this theory. It would have been the first to arrive in Ireland in postglacial times as it was accustomed to cold climates, while *autumnata* did not spread until the climate had become warmer at a later date. Being the first arrival, *filigrammaria* has had time to spread over a greater area of the country.

(d) Other First Interstadial Arrivals.

The majority of the species discussed so far in this chapter survived the second glacial phase by becoming adapted for existence in new habitats. A much larger number of species survived by becoming confined to the parts of the ice-free regions where their normal ecological conditions still existed during that glacial advance.

There are many species which have been found in Ireland only in the south-west, in Kerry or south-west Cork. It is obvious from their distributions that they must have had wider ranges in Ireland at some time in the past and that they later became confined to the glacial land south-west of that country. The same applies to species which have been found in Ireland only in the west, except that they survived on the western glacial land. It is difficult to date the probable time of arrival of many of these species with any degree of confidence. As their Irish distributions indicate that they have survived a glacial phase such species must date from one of the interstadials, but it is often difficult to judge which. Only those species for which there is additional evidence which, when taken in conjunction with their Irish distributions, indicates a probable first interstadial origin will be discussed in this section.

Apatele aceris L. is a species whose history is difficult to reconstruct because of conflicting evidence. Its distribution in Ireland, where it has been found only in the west and south-west, and the fact that it is represented in England by the apparently endemic ssp. *intermedia* Tutt, would indicate a probable first interstadial origin. But against this there is the fact that the species' chief food-plants in England are horsechestnut, sycamore and maple—trees which did not reach England until postglacial times and which are not natives of Ireland.

Possibly the species survived since first interstadial times by feeding on some trees other than these, but transferred its attention to its present food-plants when they spread into England in the post-glacial.

Taxonomic evidence also is important with *Heliophobus saponariae* Borkhausen (*reticulatus* de Villers nec Stroem). It is represented in Great Britain, where it occurs in southern England, by the ssp. *marginosa* Haworth and in Ireland, where it has been found along the south coast, by the ssp. *hibernica* Cockayne (fig. 26). This variation indicates that the Irish and the English populations have been isolated from each other for a long period of time. Probably they represent populations which survived the second glacial phase on the ice-free land south of the British Isles, west and east respectively of the river which may have flowed southwards between Ireland and Great Britain (see p. 300).

Hypena obsitalis Hübner is a suspected migrant found in the south-west of England and of Ireland. If it is a native species then its distribution indicates that it was an inhabitant of the glacial land south-west of the British Isles and its southern distribution on the Continent at the present day would indicate that it arrived at a time when the climate was at least as warm as now. Consequently it would date from the first interstadial.

Leucodonta bicoloria Schiffermüller is another suspected migrant, but its distribution seems to be natural. It has its headquarters in south-western Ireland and has been found in Great Britain only in Staffordshire, many years ago (fig. 25). Its Irish distribution indicates that it was an inhabitant of the glacial land south-west of that country and its English distribution is comparable with that of *Epicnaptera ilicifolia*. Incidentally both species have been recorded doubtfully from Devonshire.

There are several other species whose distributions indicate that they have survived since the first interstadial and which feed on plants or inhabit situations which are likely to have existed on the ice-free areas during the second glacial phase. *Jaspida pygarga* Hübner (*fasciana* auctt.), *Sterrha muricata* Hufnagel (*auroraria* Hübner), *Chloroclystis debiliata* Hübner (fig. 24), *Semiothisa notata* L., *Epione paralellaria* Schiffermüller (*vespertina* Thunberg), *Tethea fluctuosa* Hübner and *Aegeria scoliaeformis* Borkhausen (fig. 23) are examples. They have been found in Ireland only in the south-west or west, while in Great Britain they have either markedly discontinuous or south-westerly distributions. Of these, *J. pygarga* survived the second glacial phase on the glacial land south-west of England and of Ireland, *S. muricata* survived south of the ice-fronts in England and on the land west of Ireland, while the remaining species survived in these regions and also on the glacial land west of Scotland. Many of them feed on plants characteristic of cold climates, for example Birch and Bilberry, and it is possible that they first arrived in the British Isles, not during the first interstadial, but at a stage in the retreat of the ice of the first glacial phase, spreading northwards and westwards as the ice retreated.

A more widely distributed species in Ireland which probably is of first interstadial age is *Leptidea sinapis* L. It is found in England

and Wales, being perhaps most frequent in the south-west, and in the southern half of Ireland. Its relatively wide range in Ireland as compared with the ranges of the species just mentioned probably is due to its having expanded its range in postglacial times; it is one of those species which are known to undergo changes in their distributions from time to time. The chief evidence of its first interstadial origin, at least as an inhabitant of Ireland, is provided by its variation. It is represented in Ireland by the endemic ssp. *juvernica* Williams, which indicates that the Irish and English populations have been isolated from each other for a long period of time. Probably the Irish race represents a population which survived the second glacial phase on the now-submerged land in the south, while the English race represents one which survived on the land south and south-west of England. There is a possibility, however, that the English race represents a postglacial invasion of that country, this invasion not reaching Ireland.

Next there are species which have not been found in Ireland but for which evidence indicating a probable first interstadial origin exists.

The distribution of *Graptolitha furcifera* Hufnagel and *Sterrha dilutaria* Hübner indicate that they may have inhabited the glacial land south-west of England: the first species occurs as a native only in south Wales and Monmouth, while the second occurs locally in southern England but appears to have its headquarters in the south-west. The chief evidence of their relative antiquity, however, is provided by their variation. Each is represented by an apparently endemic subspecies in Britain: *G. furcifera* by the ssp. *suffusa* Tutt and *S. dilutaria* by the ssp. *holosericata* Duponchel.

Two other southern English species which are represented by apparently endemic subspecies in England are *Eupithecia pusillata* Schiffermüller, represented by the ssp. *tantillaria* Boisduval, and *Thera variata* Schiffermüller, represented by the ssp. *britannica* Turner. The two species have similar ranges in England (fig. 27) and both feed on spruce. Spruce is known to have grown in England in first interstadial times, but there is no evidence of its survival since then. The species' variation, however, indicate that they are ancient inhabitants. They and their food-plant probably survived since the first interstadial on the now-submerged land south or south-west of England.

A species whose antiquity is indicated primarily by zoogeographical evidence is *Sterrha eburnata* Wocke (*contiguaria* Hübner nec Borkhausen). It has been found only on the mountains along the north coast of Wales. It now has a southerly distribution on the Continent; which indicates that it must have arrived in the British Isles at a time when the climate was at least as warm as now, i.e., probably during the first interstadial phase. The British population probably represents one which survived the second glacial phase somewhere in the region of north Wales, the species becoming extinct elsewhere in the British Isles.

It is significant that several species are found only in the region of north Wales: *Amathes ashworthii*, *Luperina nickerlii* and *Sterrha eburnata*; that a number of the species which have markedly discontinuous distributions occur there: *Hadena caesia*, *Nyssia zonaria*,

Aegeria scoliaeformis, *Zygaena purpuralis* and the juniper-feeders; and that there are several local races confined to that region: *Eumenis semele* ssp. *thyone* Thompson and *Plebejus argus* (*aegon*) ssp. *caernensis* Thompson, for example. All these species or subspecies probably date from not later than the first interstadial phase as inhabitants of the British Isles. Their occurrence in north Wales indicates the existence somewhere in the region of north Wales of an area of relatively temperate conditions during the second glacial phase—temperate in comparison with the climate of the regions to the east and west near the ice-fronts. This region may have been situated somewhere in the bed of what is now the Irish Sea, the relatively temperate conditions being due to its low altitude in comparison with that of the glaciated areas—a region similar to that which existed in the Dogger Land at the same time and for the same reason (see p. 305).

If this was so, it is not clear why the inhabitants of that region should have spread into north Wales, as the ice retreated, the sea-level rose and the climate became warmer, but did not spread into eastern Ireland. It may indicate that north Wales became ice-free before eastern Ireland, either during the second or during the third glacial phase.

There are four excellent examples of species which do not occur in Ireland but which have wide ranges but markedly discontinuous distributions in Great Britain and probably date from the first interstadial: *Carterocephalus palaemon* Pallas, *Maculinea arion* L., *Isturgia limbaria* Fabricius (*conspicuata* Schiffermüller) and *Endromis versicolora* L.

These four species occur locally in southern England and in Scotland. The English races differ from the Scottish, which indicates that they have been isolated from each other for a long period of time. The English races probably represent populations which survived the second glacial phase south of the ice-sheets. Those of *C. palaemon* and *I. limbaria* probably survived mainly in the Dogger Land region; the first species is now found in the south only in east-central England, from Buckinghamshire to Lincolnshire, and the second only in Kent and East Anglia. The Scottish races probably represent populations which survived the second glacial phase on the land west of that country. That of *C. palaemon* was forced to change its habits in order to survive there: the Scottish race, which has been found only in western Inverness and is darker and more greenish in colour than the English race, apparently does not feed on *Brachypodium* and *Bromus*, the normal food-plants of the species, as these grasses are absent from its habitats. As mentioned above, the Scottish races of the remaining species differ taxonomically from the English. The Scottish race of *E. versicolora* tends to be comparatively richly coloured and that of *I. limbaria* tends to be large and to have relatively broad black margins on the wings. I am indebted to Professor J. W. Heslop Harrison for the information that *M. arion* has been taken in the Hebrides. Its habitats and variation there have not been recorded. In southern England, however, this species exhibits some local variation, a distinct race being found in each of the four main areas in which it occurs (see Ford, 1946). It is an inhabitant of

open country and the discontinuity of its English distribution may be due to colonies having been isolated by a development of forest. Whether or not this was the same forest development which affected the inhabitants of the Dogger Land during the second glacial phase is debatable.

Incidentally the fact that these four species are day-flying and sun-loving insects further indicates their probable first interstadial origins, as that was a time when climatic conditions favourable to them are most likely to have existed.

Chesias rufata Fabricius (*obliquaria* Schiffermüller) probably had a history similar to *I. limbaria*: it has a similar distribution in the British Isles, although it has a wider range in England, and feeds on the same plant, broom.

Finally, there are the species whose distributions and variations indicate that they invaded the British Isles in first interstadial times and again in the postglacial. Unlike species discussed previously, the first interstadial populations did not change their habits in order to survive the second glacial phase.

Before discussing these mention must be made of one species whose variation indicates that it invaded the British Isles on two occasions but whose distribution indicates that both invasions may have taken place in Pleistocene times: *Eupithecia innotata* Hufnagel. Its typical subspecies is found very locally in coastal marshes, where it feeds on *Artemisia maritima*, in eastern England, Lancashire and Cheshire. It may have had a history similar to such species as *Euchloris smaragdaria* and *Malacosoma castrensis*, except that it survived the second glacial phase in the low-lying area in the region of the Irish Sea as well as in the Dogger Land. The second subspecies is *fraxinata* Crewe, which feeds primarily on ash. It has a wider distribution in England than the typical subspecies but is most frequent in the south-westerly and westerly districts. It has been found also in the Hebrides (Canna) and in western and south-western Ireland. Its distribution indicates that it was an inhabitant of the glacial land west and south-west of the British Isles during a glacial phase. Probably it represents an invasion in second interstadial times. It is not endemic in Britain but has a wide range on the Continent. A third subspecies, the tamarisk-feeding ssp. *tamariscata* Frey, is said to have been found in Cornwall. If it occurs there as a native then it may be a survivor from the last interglacial period.

Maniola jurtina L. (*janira* L.) is an excellent example of a species which spread over the British Isles during the first interstadial and invaded the country again in the postglacial. Its typical subspecies occurs throughout most of Great Britain and in the smaller islands off the coasts. In Ireland it is represented by the endemic ssp. *iernes* Graves, in the most southerly isles of the Outer Hebrides and locally on the west coast of Scotland, it is represented by the ssp. *splendida* B.-White, while in the Scilly Isles it is represented by the ssp. *cassiteridum* Graves. These three subspecies are rather similar to each other and also resemble the southern European ssp. *hispulla* Hübner.

The probable history of *M. jurtina* as an inhabitant of the British Isles is as follows : it spread over the country during the first interstadial phase, probably at a time when the climate was rather warmer than now and when *hispulla* inhabited central Europe. During the second glacial phase a large population was isolated on the now-submerged land west and south of the British Isles, where it developed endemic racial characters. As the climate became warmer in second interstadial and postglacial times this population expanded its range and spread over most of the British Isles. It had its range split up by the rising sea, probably in late Pleistocene times. Three populations were produced by this, one in Ireland, one in Scotland and one probably in western or south-western England. Owing to their isolation from each other they developed independently, into *iernes*, *splendida* and *cassiteridum* respectively. Of these *iernes* probably has changed least, if at all, from the subspecies which developed during the second glacial phase. That is, the ancestors of the other two subspecies probably were similar to or identical with *iernes*. In postglacial times the species again invaded the British Isles, the postglacial arrivals being represented by the typical subspecies. It reached southern England over the postglacial Dogger Land and spread northwards and westwards, overwhelming the Pleistocene races by interbreeding with them so that the descendants of the latter now survive only in regions which were sufficiently isolated by the sea or, as with the western Scottish colonies of *splendida*, by mountains to prevent the postglacial arrivals from reaching them in any numbers.

There is some possibility that *Eumenis semele* L. may have had a similar history, but its variation has not been worked out fully. It tends to be large and brightly coloured in Ireland and northern Scotland, in this respect resembling the southern European ssp. *aristaeus* Bon. These forms may represent the first interstadial population, while the forms found elsewhere in Great Britain may represent the postglacial arrivals.

There are many other species whose ranges cover all or most of the British Isles and are represented by one race in the north and west and by another in the south and east. It is often difficult to judge from the literature whether these races are distinct subspecies or are merely the extreme forms of clines. However, the following appear to be examples of subspecies which probably represent the first interstadial populations of the species, the typical subspecies representing the postglacial invaders : *Cyenia mendica* Clerck race *rustica* Hübner (Ireland), *Ceramica pisi* L. ssp. *scotica* Cockayne (Scotland and Ireland), *Leucania impura* Hübner ssp. *scotica* Tutt (Scotland and Ireland), *Tethea* or *Schiffermüller* ssp. *scotica* Tutt (Scotland) and ssp. *gaelica* Kane (Ireland), *T. duplaris* L. ssp. *argentea* Tutt (Ireland), *Argynnis aglaja* L. ssp. *scotica* Watkins (Hebrides), *Euphydryas aurinia* Rottenburg ssp. *praeclara* Kane (Ireland and Hebrides) and *Polyommatus icarus* Rottenburg ssp. *clara* Tutt (Ireland and western Scotland).

Finally there are several species which have not been found in Ireland but whose distributions and variation indicate that they invaded Great Britain on two occasions.

Hydrelia flammeolaria Hufnagel (*luteata* Schiffermüller) is represented in southern English by a maple-feeding race and there is nothing to indicate that this race was anything but a postglacial arrival. The alder-feeding race, which represents the species in northern England and in Scotland, probably represents an earlier invasion. The distributions of the two races of *Aricia agestis* Schiffermüller (*astrarche* Bergstraesser) are similar: the typical subspecies occurs in southern England, while in northern England and in Scotland the species is represented by the ssp. *artaxerxes* Fabricius. Apart from the high degree of endemic variation exhibited by *artaxerxes*, good evidence of the age of the northern races of these two species is lacking. As a matter of opinion they probably developed as a result of the isolation of populations of the species on the glacial land west of Scotland during the second glacial phase and thus may date from the first interstadial. The easterly distributions of *artaxerxes* in Scotland at the present day might indicate that it survived the third glacial phase on the land east of the ice-fronts in that region. Incidentally interbreeding between the postglacial arrivals and the Pleistocene populations of this species has taken place where their ranges meet in northern England, intermediate forms ("salmacis" etc.) being found there. Similar interbreeding has taken place where the ranges of the typical subspecies and the ssp. *splendida* of *Maniola jurtina* overlap in western Scotland.

The typical subspecies of *Argynnis selene* Schiffermüller probably was a postglacial arrival, but the distribution of the ssp. *insularum* Harrison indicates that it was an inhabitant of the glacial land west of Scotland and thus that it is of Pleistocene age. It is found in certain islands of the Hebrides and probably dates from the first interstadial phase.

VII. THE ARRIVALS OF THE SECOND AND THIRD GLACIAL PHASES.

In the British Isles the ice-sheets of the second glacial phase were less extensive than those of the first, while the ice-sheets of the third glacial phase were less extensive than either. The maximum of the first glacial phase was about 115,000 years ago, that of the second glacial phase was about 27,000 years ago and that of the third about 22,000 years ago. It is apparent from this that the second interstadial phase was short in comparison with the first. Furthermore geological evidence indicates that its climate was not as warm as that of the first or of the postglacial. The first glacial phase arrivals had to survive two relatively long and temperate periods, which must have affected their ranges and distributions: the first interstadial phase and the postglacial. The second and third glacial phase arrivals had to survive only one: the postglacial. The climatic and vegetational changes of the second interstadial probably had little effect on the ranges and distributions of most of the second glacial phase arrivals in comparison with the effects of the postglacial changes. Consequently it is often difficult to distinguish the second from the third glacial phase arrivals on zoogeographical grounds, and because of the comparatively short time which elapsed between their arrivals no well-marked line of distinction between them is provided by

taxonomic evidence. For these reasons it is frequently impossible to date the time of arrival of many of the species discussed in this chapter apart from saying that they arrived during one or the other, or during both, of the last two glacial phases of the Upper Pleistocene glaciation.

At their maximum the ice-sheets of the second glacial phase⁵ were less extensive than those of the first. Most of England south of Yorkshire and most of the south coast counties of Ireland were ice-free (fig. 1). As the sea-level probably was at least 300 and perhaps more than 400 feet lower than now there must also have been extensive areas of ice-free land off the present coasts of the British Isles. The ice-sheets retreated slowly and during their recession prolonged halts and even readvances of the ice-fronts occurred.

The British ice-sheets of the third glacial phase⁶ were much less extensive than those of the second. A large ice-sheet covered most of Scotland, except the east, and extended to reach north-western England, the Isle of Man and north-eastern Ireland (fig. 1). Smaller ice-sheets existed on the mountains of Ireland and probably also on the mountains of Wales and of northern England. The sea-level was still considerably lower than now in relation to the land, except in the region of western Scotland and north-western Ireland where an isostatic sinking of the land had taken place due to the great weight of the Scottish ice-sheet.

(a) *The Alpine and Northern European Species.*

It may be concluded that all or most of the Alpine and northern European species of Lepidoptera probably arrived in the British Isles not later than the second glacial phase. The reason for this is that during that glacial phase the British ice-sheets were in contact with the northern European,⁷ so that a belt of land on which ecological conditions were favourable to those species must have extended from north-central Europe into the British Isles, south of the British and northern European and north of the Alpine ice-sheets⁸ (fig. 2). During the third glacial phase, however, the British ice-sheets were not in contact with those of the Continent but were separated by regions in which relatively temperate climatic conditions existed—regions where conditions were ecologically unfavourable to the northern European and Alpine species and which may have formed an effective barrier to their migration into the British Isles.

Two species appear to have arrived from the Alpine region: *Erebia aethiops* Esper and *Zygaena exulans* Hoch. The origin of the first species is shown by the fact that it is confined to the mountains of central Europe at the present day; that of the second by its being represented in the British Isles by the ssp. *subochracea* B.-White, which is said to

⁵ Also known as the New Drift and Ivernian ice-sheets. The Third Glacial Period of Stamp (1946). Apparently not mentioned by Ford (1945).

⁶ Also known as the Valley Glaciation or Zone III late-glacial period. The Fourth Glacial Period of Stamp (1946). Apparently the Fourth Pleistocene Glaciation of Ford (1945).

⁷ The Weichsel (Brandenburg).

⁸ The Würm II ice sheets.

resemble an Alpine race of the species. *E. aethiops* inhabits the mountains of northern England and of Scotland and may have survived the third glacial phase on the western glacial land, the colony found in north-western Yorkshire which exhibits distinct subspecific characters representing a population which survived somewhere to the south-east of the Scottish ice. *Z. exulans* has been recorded only from the mountains of Aberdeenshire (fig. 28) and this colony may represent a population which survived the third glacial phase east of the Scottish ice-sheet.



FIGS. 28-33.—Types of ranges of second and third glacial phase Lepidoptera.

The origins of these two species are difficult to reconstruct, and it is quite possible that both date from the first, rather than from the second, glacial phase.

The species which now have Boreo-Alpine distributions on the Continent may have spread into the British Isles from the northern European, rather than from the Alpine, region. As with the Boreo-Alpine species discussed in Chapter V, this conclusion is based largely on negative evidence: none shows any taxonomic or other evidence of having spread from the Alpine region and their ranges and distributions

in the British Isles indicate that they have had rather different histories from the species for which evidence of an Alpine origin does exist.

The species in question all have comparatively wide ranges in the British Isles but have their headquarters in the mountains of the north and west. Some may date from the first glacial phase, at least originally, as they occur in islands which are unlikely to have been connected by land to other regions later than early in the first interstadial phase. They include *Xanthorhoë munitata* Hübner and *Entephria caesiata* Schiffermüller (*annosata* Zetterstedt) (fig. 32), which are found in St. Kilda, the Faroes and Iceland, and *Celanea haworthii* Curtis, found in the Faroes. Whether or not these three species are wholly of first glacial age is debatable. If they are, then the climate and vegetational changes of the first interstadial affected them to a much lesser degree than they affected other first glacial phase arrivals. It is perhaps more probable that they invaded the British Isles during the first glacial phase and again during the second.

Pylarge fumata Stephens (? *ternata* Schrank) has a contradictory type of distribution in the British Isles (fig. 30): it inhabits the northern and western parts of Great Britain but has been found in Ireland only in the south. One explanation for this is that the species may have spread into the southern parts of the British Isles when the ice-sheets of the second glacial phase were at their maximum. As the ice retreated the species spread northwards in Great Britain but, for some unknown reason, did not follow the retreating ice northwards in Ireland. An alternative explanation is that, like many Pleistocene species, it became extinct over most of its original range in Ireland some time near the end of the Ice Age (see p. 325).

Other Boreo-Alpine species which probably date from the second glacial phase are *Ammogrotis lucerneae* L., *Dasypolia templi* Thunberg, *Hadena glauca* Hübner (? *bombycina* Hübner) (fig. 31), *Hydriomena ruberata* Frey, *Venusia cambrica* Curtis and *Calostigia olivata* Schiffermüller.

All the above Boreo-Alpine species have been found in Ireland. The ranges of *A. lucerneae* and *E. caesiata* cover the whole of that country and their distributions there are obviously regulated by the distribution of ecologically suitable habitats. Apart from *P. fumata*, all the remaining species have ranges which cover only the northern half of that country with, except in the cases of *D. templi* and *X. munitata*, isolated colonies in the south-west. Their northerly distributions might be due to present-day climatic conditions—to the lower average annual temperatures of most of the northern half of the country. But if this is so then the species might be expected to be more widely distributed on the mountains in the south where the average temperatures are equally low—they might be expected to be as widely distributed as *E. caesiata*. A more likely explanation is that their northerly distributions are due to their having spread into Ireland only in comparatively recent times from a northerly direction. It will be shown later that the only postglacial land-connection between Great Britain extended

between western Scotland and northern Ireland (pp. 355-6). The distributions of these species are consistent with their having arrived in Ireland via this land-connection, spread over the northern half of the country and were prevented from spreading into the mountains of the south by the warmer climates of the Central Plain. They probably inhabited Ireland at an earlier date but became extinct in most parts of the country before the end of the Ice Age. Their south-western Irish colonies may be survivors of the first invasion. If it is found that the south-western Irish colonies differ taxonomically from the inhabitants of the northern half of the country it will be a strong indication that the theory of their different origins is correct ; at present there is no information on this point.

There is an additional Boreo-Alpine species which may have been a second glacial phase arrival : *Comacla senex* Hübner. Unlike the species discussed above, its headquarters are not in the northern and western parts of the British Isles. It has been found in England south of Yorkshire, in southern Perthshire and in Ireland in Fermanagh, Wicklow and Waterford. Its discontinuous distribution indicates its antiquity as an inhabitant of the British Isles. The species may have spread over the British Isles during the second interstadial phase, having arrived during the second glacial phase undergone numerous local extinctions during the third glacial phase and not have altered its distribution since.

(b) *The Northern British Species.*

In this section are discussed the remaining species which have northerly or northerly and westerly distributions in Great Britain. This type of distribution indicates that they invaded the country at a time when the climate was colder than now, a fact also indicated by the preference of the majority for heaths or other habitats characteristic of cold climates and by their northern and central European distributions on the Continent at the present day.

Of these species *Perizoma blandiata* Schiffermüller (*adaequata* Borkhausen) occurs in the Faroes and *Plusia interrogationis* L. occurs in St. Kilda and Iceland. This indicates that these two species spread over the British Isles during or immediately following the first glacial phase, but their wide distributions and lack of marked local variation in the British Isles would indicate that they invaded the country again at later dates—perhaps during both the second and the third glacial phases.

In some cases antiquity is indicated by taxonomic evidence. In the case of *Apatele menyanthidis* Vieweg and *Ctenonympha tullia* Müller (*tiphon* Rottenburg, *davus* Fabricius) the variation is particularly marked and is in the form of clines. The first species grades from the race *scotica* Tutt in Scotland and Ireland to the typical race in northern England and the second grades from the race *scotica* Tutt in Scotland via the race *tullia* to the race *philoxenus* Esper in northern England. It would seem probable that both species date from not later than the second glacial phase as inhabitants of the British Isles.

Dasychira fascelina L. and *Operophtera fagata* Scharfenberg (*boreata* Hübner) have ranges in Ireland which cover only the northern half of the country. This may mean that, like species discussed in the last section, they invaded Ireland from Scotland in postglacial times, having previously become extinct in Ireland. Both probably date from the second glacial phase as inhabitants of Great Britain. *Lithomoia solidaginis* Hübner is the only species discussed in this section which has not been found in Ireland. It may have had a history similar to *D. fascelina* and *O. fagata* except that it did not re-invade Ireland in the postglacial. From analogy with other species it would seem likely that it did inhabit Ireland in Pleistocene times but became extinct there before the end of that period. *Eurois occulta* L. and *Hyppa rectilinea* Esper obviously must have had wider ranges in Ireland at some time in the past than they have at present: the first species has been found in Ireland only in Derry and Sligo (fig. 29), the second only in Kerry. If they became extinct over the greater part of their original ranges in Ireland, it is reasonable to assume that *L. solidaginis* could have become wholly extinct in that country—far more reasonable than to assume that it never inhabited Ireland.

Other species which have northerly or northerly and westerly ranges and probably date from the second glacial phase include *Plusia bractea* Fabricius, *Epirrhoë tristata* L. and *Lygris populata* L.

The majority of the species discussed above exhibit some sort of local variation in the British Isles, which further indicates their relative antiquity. Incidentally the fact that *L. populata* is found both in damp woods, where it feeds on *Salix*, and on heaths and bogs, where it feeds on bilberry and crowberry, might indicate that, like the closely-related *L. testata* (p. 312), it is represented by two races in the British Isles, one dating from the first interstadial phase, the other from late-glacial or early postglacial times. The variation of this species requires further investigation.

There is now the question of why such species as *Eurois occulta* and *Hyppa rectilinea*, and probably also *Hadena glauca*, *Celaena haworthii*, *Pylarge fumata*, *Hydriomena ruberata*, *Venusia cambrica* and *Perizoma taeniata*, apparently became extinct in most parts of Ireland before the end of the Ice Age and why such species as *Lithomoia solidaginis*, *Dasypolia templi*, *Dasychira fascelina*, *Operophtera fagata*, *Xanthorhoë munitata*, *Carsia paludata* and *Coenocalpe lapidata* may have become totally extinct there, although all these species remained widely distributed in Great Britain.

One explanation is that they may have become extinct in many parts of Great Britain at the same time, but invaded that country again towards the end of the Pleistocene or in early postglacial times. For several reasons this is improbable. Some of the above species have Boreo-Alpine distributions abroad and therefore are unlikely to have been able to have invaded the British Isles later than the second glacial phase (see p. 321). In no case does taxonomic evidence indicate that a species is a more ancient inhabitant of Ireland than of Great Britain, while in many cases species exhibit equal degrees of endemic variation

in both countries. Finally, if they had spread into Great Britain in third interstadial times they could have spread into Ireland before the end of the Ice Age as, owing to the eustatic lowering of the sea-level, it is probable that the two countries were connected by land in the south. But none of the species appears to have spread into Ireland in that way.

A more reasonable explanation is to assume the former existence in Ireland, but not in Great Britain, of some environmental conditions which were unfavourable to the species and which caused their extinctions in the former country. The present ranges of the species in Great Britain provide a clue to the possible nature of these conditions. Unlike the majority of the remaining second glacial phase arrivals, the majority of the species in question have northerly, as distinct from northerly and westerly, distributions in Great Britain. This would indicate that they like low average annual temperatures coupled with cold winters. The unusual, northerly and easterly, distributions of *E. occulta* and *D. fascelina* particularly indicate this. At the present time both the average annual and the winter temperatures are higher over most of Ireland than over most of northern England and Scotland. Perhaps at some time near the end of the Pleistocene the climate of Ireland may have been more oceanic in relation to that of northern England and of Scotland than at present, and this may have been sufficient to cause the extinction of the species over all or most of Ireland. This is not unlikely to have been the case, as when Great Britain was connected by land to the Continent its climate must have been more continental than now and its average annual temperatures are likely to have been low because of the proximity of the northern European ice-sheets. On the other hand, the climate of Ireland must have been relatively oceanic because of the effects of the sea and because of its distance from the major ice-sheets. At the time of the extinctions of the Lepidoptera in question the climate of Ireland must have been more oceanic than it has been since the postglacial Irish-Scottish land-connection existed, as otherwise the postglacial invaders would not have survived.

There still remains to be discussed a number of additional species which have mainly northerly or northerly and westerly distributions in Great Britain. Unlike those discussed above, however, they do not appear to have mainly northern distributions on the Continent.

Hydraecia crinanensis Burrows, *H. lucens* Frey, *Oporinia christyi* Prout and *Ortholitha scotica* Cockayne (see p. 278) appear to have northerly distributions in Great Britain and have ranges which appear to cover the whole of Ireland. This would indicate that they were glacial phase arrivals, but as their distributions abroad are unknown and their British distributions probably have not yet been worked out fully it is impossible to reconstruct their histories at present.

Rhyacia simulans Hufnagel (*pyrophila* Schiffermüller) has been found in Ireland only in Sligo, *Amathes depuncta* L. has not been found in Ireland, and *Antitype chi* L. is confined to the northern half of that country. These may be further species which became extinct in Ireland before the end of the Pleistocene, except for *R. simulans*, which survived

locally in the west. *A. chi* may have re-invaded Ireland from the north in postglacial times.

Xylophasia furva Schiffermüller and *Calostigia salicata* Hübner occur in the Shetlands and thus probably spread over the British Isles before the end of the Pleistocene, as the Shetlands probably were not connected to the mainland by land in postglacial times. Their distributions in the British Isles may be regulated largely by the distributions of ecologically suitable habitats, rocky situations and hills respectively. It is difficult to arrive at any more definite conclusion on the probable dates of arrival of these three species. *C. salicata* appears to be especially characteristic of the mountains of central Europe and thus possibly may have arrived with the Alpine species during the second glacial phase.

Next there are species which have northern and central European distributions on the Continent and which frequent birchwoods, heaths or other habitats characteristic of cool or cold climates but which, unlike the species discussed above, have ranges which cover the whole of Great Britain, although the species tend to be more scarce in the south and east than in the north and west.

Of these, *Charaëas graminis* L. is found in Iceland and St. Kilda and thus probably spread over the British Isles during or immediately following the first glacial phase. Most probably it invaded the British Isles during each of the three Upper Pleistocene glacial phases at the times when steppe conditions prevailed. *Parasemia plantaginis* L., which has a wider range on the Continent, may have had a similar history as a British species; it occurs in St. Kilda.

Achlya flavicornis L. exhibits some local variation in the British Isles. It is represented in Scotland by the race *scotica* Tutt which may represent a different, and earlier, invasion from that represented by the typical subspecies. It is said to be very similar to the northern European race *finmarchia* Schöyen and in Britain may represent a second glacial phase population, the typical race representing a later invasion, probably one during the third glacial phase.

Other species which probably date from one of the glacial phases, and most probably from the third, are *Plusia v-aureum* Hübner (*pulchrina* Haworth), *Eulype hastata* L., *Pheosia gnoma* Fabricius (*dictaeoides* Esper) and *Cerura furcula* Clerck.

Then there are several species which have habits and distributions in the British Isles similar to those just discussed, but which apparently have not got northern and central European distributions abroad, the majority having ranges which cover most of Europe.

Of these, *Amathes glareosa* Esper and *Eumichtis adusta* Esper occur in the Shetlands and develop local forms in parts of the British Isles. This indicates that they are at least of third glacial phase age as inhabitants of the British Isles, but it is difficult to reconstruct their histories more definitely. Possibly some of their local varieties, for instance the form *rosea* Tutt of *A. glareosa*, may represent relatively early invasions. *Amathes agathina* Duponchel and *Diarsia dahlîi* Hübner also tend to

exhibit some local variation. The former species has a mainly northerly distribution in Ireland, which may indicate that it invaded that country in postglacial times, having become extinct there at an earlier date. The two species probably date from the Pleistocene as inhabitants of the British Isles and possibly date from the second glacial phase, the first species perhaps from the second interstadial. The histories of such species as *Diacrisia sannio* L. (*russula* L.) and *Gymnoscelis pumilata* Hübner are difficult to reconstruct. As a matter of opinion it would seem likely that they date from the latter part of the Upper Pleistocene—perhaps from the third glacial phase.

Finally there are five species which are characteristic of maritime habitats, although occurring also in certain habitats inland, and have their headquarters in the northern and western parts of Great Britain. Because of their maritime habits they may have been less affected by past climatic changes than inland species and thus their histories are rather more difficult to reconstruct.

The variation of *Aporophyla lutulenta* Schiffermüller may indicate that it invaded the British Isles on more than one occasion. It is represented in Ireland and Scotland and locally in north-western England and north Wales by a race comprising the forms *luneburgensis* Frey and *sedii* Guenée. The distribution of this race in Ireland—where the species has been found only in the north-west—and in Great Britain might indicate that it represents a population which inhabited the glacial land west of Scotland and north of Ireland. The species has a wide range on the Continent and thus may not necessarily have been a glacial phase arrival in the British Isles. Possibly it dates from the first interstadial phase, the race *luneburgensis-sedii* developing during the second glacial phase. The typical race of the species is found in the southern parts of Great Britain and may represent a more recent invasion.

The occurrence of *Hadena conspersa* Schiffermüller (*nana* Rottenburg) in the Shetlands indicates its Pleistocene origin. Some degree of relative antiquity also is indicated by the considerable local variation it exhibits in many parts of its range in the British Isles. Otherwise it is difficult to date and may have invaded the country on more than one occasion. Similarly, *Stilbia anomala* Haworth, *Procus furunculus* Schiffermüller (*bicolorius* de Villers) and *Aporophyla nigra* Haworth probably spread over the British Isles before the end of the Pleistocene, perhaps on more than one occasion. For reasons to be explained later, *S. anomala*, like *A. agathina*, may have been an interstadial rather than a glacial phase arrival.

(c) Other Glacial Phase Arrivals.

Many of the species whose ranges cover all or most of the British Isles and which are characteristic of heathy localities of one sort or another, but which are not more frequent in the north and west than in the south and east, may have invaded the British Isles during glacial phases. This applies particularly to species which have northern and central European distributions on the Continent.

Of these, *Dysstroma citrata* L. (*immanata* Haworth) occurs in Iceland, *Eupithecia nanata* Hübner occurs in the Faroes and *Hepialus fusconebulosus* Degeer (*velleda* Hübner) in St. Kilda. The three species exhibit some local variation in the British Isles, that of *D. citrata* being rather extensive. Their occurrence in the Atlantic islands indicates that they spread over the British Isles on the retreat of the ice of the first glacial phase and it is probable that they invaded the country again during both of the subsequent glacial phases. Other species which probably were Pleistocene arrivals, dating from the third and probably from earlier glacial phases in addition, include *Lycophotia porphyrea* Schiffermüller (*strigula* Thunberg, *varia* de Villers), *Amathes castanea* Esper (*neglecta* Hübner), *Parastichtis suspecta* Hübner, *Hadena contigua* Schiffermüller, *Trichopteryx carpinata* Borkhausen (*lobulata* Hübner), *Calostigia multistrigaria* Haworth and *Drepana falcataria* L. (*falcula* Schiffermüller).

Polia tincta Brahm has a range, both in Great Britain and abroad, similar to these species and inhabits birchwoods and heaths. However, it has not been found in Ireland. Possibly it was a second glacial phase arrival which later became extinct in that country.

Virtually all the glacial phase arrivals discussed above and in Chapter V invaded southern England in the first instance and later spread northwards and westwards over the British Isles as the ice-sheets retreated, most of them eventually becoming extinct in the south when the climate there became unfavourably warm. However, there are some species which probably were glacial phase arrivals and which did not spread northwards and westwards to any extent as the ice-sheets retreated, but remained confined to the regions in the south which were ice-free at the time they invaded the British Isles.

Firstly there are three species which have been found in western Europe only in the north, in the Baltic region. They must have been forced southwards by glaciations of that region and then spread westwards into the British Isles. The three species in question are *Arenostola elymi* Treitschke, *A. morrisii* Dale (*bondii* Knaggs) and *Caenophila subrosea* Stephens.

C. subrosea was found in the British Isles only in the Fenlands of East Anglia. It was represented there by its typical subspecies which has been found abroad only in Denmark, the normal Continental race being the ssp. *subcaerulea* Staudinger. The ssp. *subrosea* probably has had a similar history as a British species to such species as *Eilema pygmaeola*, *Lycæna dispar* and other Dogger Land inhabitants (see p. 304). It certainly is of Pleistocene age and probably dates from the second glacial phase. The ssp. *subcaerulea* probably represents a population which spread into northern Europe from a south-easterly direction after the retreat of the last ice-sheets from the Baltic region.

A. elymi, on the other hand, probably is a comparatively recent arrival. Its distribution in the British Isles indicates that it spread westwards along the north coast of the Dogger Land at a time when that land was no more extensive than it was in early postglacial times: it is

found on the east coast of Great Britain from Norfolk to Fife (fig. 33). There is thus nothing to indicate that the species arrived in England earlier than at a late stage of the third glacial phase or in postglacial times. On its arrival via the north coast of the Dogger Land it spread northwards up the east coast of Great Britain. However, it has been recorded from Sussex and south Devon, and if these records are correct then they would indicate that it has a more ancient history as a British species.

A. morrisii probably was a Pleistocene arrival which, like *C. subrosea*, was forced southwards on the Continent by a glaciation of northern Europe. It occurs on the coasts of the Baltic and on the south coast of England. As a matter of opinion it would seem likely that it dates from at least the second glacial phase as an inhabitant of England.

Incidentally this species, *Arenostola elymi* and *Luperina nickerlii* probably are representatives of the steppe fauna which inhabited north-central Europe during the latter part of each glacial phase. They occur only in that region and inhabit situations on sandy soils. Probably they developed as species by the isolation of populations of their ancestors in that region, these populations becoming adapted for life on the loess steppes. On the disappearance of steppe conditions from western Europe they became confined to sandy coasts, the situations where ecological conditions are now most favourable to them.

Bomolocha crassalis Fabricius (*fontis* Thunberg) and *Calocalpe undulata* L. have northern and central European distributions abroad and are characteristic of heathy situations. It is therefore not unlikely that they were glacial phase arrivals. Their present distributions in the British Isles indicate that they were inhabitants of the glacial land to the south and west: the first species is found all over Ireland and in the south-western and western parts of England and Wales, while the second is found in England and south Scotland and in southern and western Ireland. Probably they arrived during the second glacial phase, spread over the British Isles as the ice retreated and then were confined to the southern and western parts of the British land-mass during the third glacial phase.

Parascotia fuliginaria L., *Sterrhia sylvestraria* Hübner (*straminata* Treitschke), *Brephos parthenias* L. and *Cerura bicuspidis* Borkhausen probably also were glacial phase arrivals, as they inhabit heathy situations and have northern and central European distributions abroad. Their very local distributions indicate some degree of relative antiquity. All are confined to England and may have spread into that country during a glacial phase but, unlike most other glacial phase arrivals, did not move northwards as the ice retreated. It is difficult to date them with any certainty; possibly they were second glacial phase arrivals.

It is quite possible that some of the species—those characteristic of heathy situations—included in Chapter IX may date from the third or even from an earlier glacial phase. Of these, *Cosymbia pendularia*,

Dyscia fagaria and *Gnophos obscurata* are the best examples, as they exhibit local variation and the first two appear to have mainly northerly and westerly distributions in the British Isles. Other examples are *Anarta myrtilli*, *Sterrhia inornata*, *Calostigia multistrigaria*, *Ectropis punctulata*, *Ematurga atomaria*, *Pachycnemia hippocastanaria* and *Saturnia pavonia*. It is possible, however, that some of these date from the Pre-Boreal postglacial period.

VIII. OTHER PLEISTOCENE ARRIVALS.

There are many other species for which evidence indicating a Pleistocene origin exists. A large proportion of them may date from the first interstadial phase, but the evidence for this is not so strong as with the species discussed in Chapter VI. The remainder probably were either second interstadial arrivals or arrived during both interstadial phases.

The second interstadial phase⁹ was of comparatively short duration in comparison with the first: some 88,000 years elapsed between the maxima of the first and second glacial phases, while only about 5,000 years elapsed between the maxima of the second and third. During the second interstadial phase the ice disappeared from the British Isles, except possibly from the western Highlands of Scotland. Cool temperate climatic conditions prevailed and, in eastern Ireland at least, there was open countryside with an abundance of grasses and herbaceous plants and with scattered trees. The sea-level probably was lower than now, as there were still extensive ice-sheets abroad.

(a) *The Maritime Species.*

Species characteristic of the sea-coasts may be more ancient inhabitants of a country than their present wide ranges and distributions may be thought to indicate. The reason for this is that owing to the effect of the sea in reducing the annual range of temperatures of the sea coasts such species may have been able to survive unfavourable climatic periods which caused the extinction in many regions of inland species. Unlike those discussed in Chapter VI, none of the maritime species discussed here appears to inhabit situations in the British Isles which differ ecologically from those they inhabit on the Continent.

Euxoa obelisca Schiffermüller has a wide range in the British Isles, but has its headquarters in the southern and western districts. Its distribution is such as to indicate that it survived the second glacial phase on the coasts south and west of the British Isles and to the east of the Highland ice-sheet. Its relative antiquity is further indicated by the local forms it has developed in parts of the British Isles. Probably it is at least of second interstadial age. *Leucania littoralis* Curtis and *Orthosia advena* Schiffermüller (*opima* Hübner) may have had similar histories as they too have their headquarters on the southern and western coasts.

⁹ Also known as the Zone II late-glacial period or the Allerød Oscillation. The Third Interglacial Period of Stamp (1946) and apparently of Ford (1945).

The occurrence of *Heliophobus sordidus* Borkhausen (*anceps* Hübner) in the Shetlands indicates that it spread over the British Isles before the end of the Pleistocene. Its occurrence in Ireland only in Dublin is not easy to explain, but from analogy with other species which, like this, have wide ranges in Great Britain but are very local in or absent from Ireland (see p. 335) it may be concluded that it probably was a second interstadial arrival.

Miana literosa Haworth, *Euxoa nigricans* L., *Agrotis vestigialis* Hufnagel (*valligera* Schiffermüller) and *Epirrhoë galiata* Schiffermüller



FIGS. 34-39.—Types of ranges of second interstadial phase Lepidoptera.

are found around the coasts of the British Isles and occur inland in Ireland on the shores of Lough Neagh. They probably spread into that region at a time when Lough Neagh was in direct connection with the sea. This is likely to have been the case during the third glacial phase when the land in that region was lower than now in relation to the sea due to an isostatic sinking as a result of the weight of the Highland ice-sheets. Thus it is probable that these four species spread over the British Isles during the preceding second interstadial phase. The Pleistocene

age of *E. nigricans* is further indicated by its occurrence in the Shetlands and some degree of antiquity is also indicated by the local variation exhibited by the above species, with the apparent exception of *M. literosa*. Incidentally the distributions of these species in north-eastern Ireland, particularly that of *M. literosa*, indicates that Lough Neagh probably was connected to the sea in the north, along the valley of the present River Bann (Beirne, 1944).

The considerable local variation exhibited by *Euxoa cursoria* Hufnagel and *Agrotis clavis* Hufnagel (*corticea* Hübner) indicate that they too probably are relatively ancient inhabitants of the British Isles. Both probably date from at least the second interstadial phase, the Pleistocene origin of the first species being further indicated by its occurrence in the Shetlands.

It is quite possible that some or all of the above species invaded the British Isles during both interstadial phases, but it is doubtful if any dates wholly from the first.

(b) The Local Irish Species.

These are species whose Pleistocene origin is indicated primarily by their distributions in Ireland. The majority are confined to the south, west or south-west of that country and thus probably were inhabitants of the now-submerged glacial land. They must have had wider ranges in Ireland at some time in the past, and it is very improbable that the climatic and vegetational changes of the later postglacial could have been responsible for their present restricted ranges there. Consequently it may be concluded that they were Pleistocene arrivals.

Firstly there are some twenty species whose ranges in Great Britain do not extend north of the southern Uplands of Scotland, most of them being confined to the southern half of England. The majority are woodland species but are not characteristic of types of woodland which are likely to have existed on the ice-free areas of the British Isles during the second glacial phase. The only possible exceptions are the lichen-feeding species *Eilema deplana* Esper (*depressa* Esper), *E. sororcula* Hufnagel and *Mittochrista miniata* Förster. In Ireland the second of these has been found only in the Burren district, the other two only in Kerry. Possibly they date from the first interstadial but more probably date from the second. *E. deplana* may have invaded the British Isles on two occasions, the form *unicolor* Bankes, which represents the species in Ireland and is frequent in parts of southern England, perhaps representing a first interstadial invasion, the typical form a second interstadial or a postglacial invasion. The remaining species probably were second interstadial arrivals. In no case is any greater antiquity indicated by taxonomic evidence or by their distributions in England. They include *Earias clorana* L. (fig. 34), *Cucullia verbasci* L., *Herminia barbalis* Clerck, *Lymantria monacha* L., *Eupithecia pimpinellata* Hübner (*denotata* Guenée nec Hübner), *Philereme vetulata* Hübner, *Ectropis consonaria* Hübner, *Boarmia punctinalis* Scopoli (*consortaria* Fabricius), *Bapta bimaculata* Fabricius, *Stauropus fagi* L. and *Melitaea athalia*

Rottemberg, found in Ireland only in the south-west, in Kerry or south-west Cork, *Panemeria tenebrata* Scopoli (*arbuti* Fabricius), found in Ireland only in the west (Kerry and Sligo), *Cepphis advenaria* Hübner, found in Ireland only in the south (Limerick and Waterford) and *Angerona prunaria* L., *Thecla betulae* L. (fig. 35) and *Gonepteryx rhamni* L., which have wider ranges in Ireland but are confined to the south and west.

About a dozen species have ranges in Ireland similar to those just discussed but have wider ranges in Great Britain. Of these there is a possibility that *Amathes ditrapezium* Borkhausen and *Euphyia cuculata* Hufnagel may be of first interstadial age. Both have markedly discontinuous distributions in Great Britain, occurring in southern England and in the Scottish Highlands. In Ireland both have been found only in the Burren region. Possibly the Scottish and the Irish populations represent populations which survived the second glacial phase on the western glacial land, the English population representing one which survived south of the ice-sheets. Their ecology does not contradict this: the first species inhabits birchwoods, the second open country. *Tholomiges turfosalis* Wocke and *Odontesia carmelita* Esper possibly are of the same age. They have wide ranges, but very local distributions, in Great Britain and have been found in Ireland only in Kerry. On ecological grounds it is possible that they could have survived the second glacial phase: the first species inhabits bogs and heathy marshes, the second birchwoods. On ecological grounds it seems unlikely that any of the remaining species could have survived the second glacial phase. As their distributions in Ireland indicate that they were not postglacial arrivals, in that country at least, it may be concluded that they date from the second interstadial phase. The occurrence of *Triphaena orbona* Hufnagel (*subsequa* Schiffermüller) in the Shetlands further indicates its Pleistocene origin. *Craniophora ligustri* Schiffermüller exhibits considerable local variation, apparently in the form of a cline, which indicates some degree of relative antiquity. Its second interstadial age is further indicated by analogy with *Eupithecia innotata* ssp. *fraxinata* as, like that race, it feeds on ash and has been found in Ireland only in the west. Other species included here which probably are of second interstadial age are *Epirrhoë rivata* Hübner and *Argynnis euphrosyne* L. (fig. 36), which have been found in Ireland only in the Burren region, *Cleora glabraria* Schiffermüller (*jubata* Thunberg) and *Drymonia dodonaea* Schiffermüller (*trimacula* Esper), found in Ireland only in the south-west, *Sesia apiformis* Clerck, found only in southern Ireland, and *Erynnis tages* L., found in the south and west.

While these species probably are at least of second interstadial age as inhabitants of Ireland, and perhaps of Scotland, there is a possibility that some of them may have invaded England again in post-glacial times. This may explain why most of them are widely distributed in southern England. However, definite evidence of postglacial invasions is lacking.

It is significant that the species discussed so far in this section, as well as many of the first interstadial arrivals, have had their ranges in

Ireland greatly reduced before the end of the Pleistocene, while their ranges in Great Britain were little affected. It will be recalled that some of the glacial phase arrivals were affected in the same way (p. 325), but the factors which affected them unfavourably—relatively warm winters and relatively high average annual temperatures during the second interstadial—would not have been detrimental to the species under discussion as they would find such conditions not unfavourable. However, the same explanation may apply to both groups of species—a relatively oceanic climate in Ireland before the end of the Pleistocene. An oceanic climate implies that the summers are relatively cool and damp and this is what may have affected the first and second interstadial arrivals in Ireland. Some evidence for this is provided by the fact that many of them are day-flying and sun-loving species or frequent dry situations, examples being *Argynnis euphrosyne*, *Melitaea athalia*, *Erynnis tages*, *Panemeria tenebrata*, *Eupithecia pimpinellata*, *Euphyia rivata*, *E. cuculata*, and *Sesia apiformis*, as well as *Setina irrorella*, *Phothedes captiuncula*, *Nyssia zonaria* and *Zygaena purpuralis*. A period when the summers were relatively cool and wet in Ireland as compared with Great Britain, the contrast being greater than at the present day, could have caused their extinction over most of Ireland. As many of these species probably spread over Ireland during the second interstadial phase it may be concluded that it was during the third glacial phase that these conditions existed.

Some confirmatory evidence is provided by the fact that many of these species have survived in Ireland only in an exceptionally well-drained region—the Burren and adjacent limestone areas of Clare and south Galway. The terrain there consists typically of bare limestone pavements traversed by numerous fissures in the bottoms of which grow a remarkable assemblage of plants. The ecoclimatic conditions prevailing at the bottom of these fissures, notably the dryness of the shallow and well-drained soil, may have permitted the species to survive the unfavourable climatic period which exterminated them elsewhere in Ireland.

However, there are many species whose restricted ranges in Ireland are unlikely to have resulted from a period of wet summers as they are species which inhabit damp situations or feed on moisture-loving plants such as lichens, or at least do not show any evidence of requiring dry summer weather. With them the temperature during the third glacial phase, rather than the rainfall or humidity, may have been the chief detrimental factor.

The reason why the larger number of the species which have had their ranges restricted are now to be found in the south-west of Ireland is less easy to explain. It may be due to the summers on the now-submerged land south of Ireland having been sufficiently warm during the third glacial phase to have enabled the species to have survived there. The reason the summers may have been relatively warm there is that the average annual temperatures probably were sufficiently high, because of the southerly latitudes, to overcome the effects of the low annual range

of temperature, as far as the Lepidoptera were concerned. An alternative explanation is that as the climate in the neighbourhood of an ice-sheet tends to be more dry than that of regions farther away, conditions favourable to the species may have existed in Ireland during the third glacial phase mainly in the region of Kerry because the Kerry ice-sheet seems to have been the most extensive of the Irish ice-sheets at that time. Probably both factors were operative. Most probably, however, future geological investigations will throw more light on this question.

As the above species probably became extinct over the greater part of their original ranges in Ireland it is reasonable to assume that other species became wholly extinct there during the unfavourable climatic phase. Likely examples are *Isturgia limbaria*, *Endromis versicolora*, *Argynnis selene*, *Maculinea arion* and *Carterocephalus palaemon*; other possible examples will be discussed later (p. 339).

To return to the possible second interstadial arrivals; there is a considerable number of species which have wider ranges in Ireland than those discussed above. They are species whose ranges cover the southern half of Ireland or which are widely distributed over the southern half but are very local in the north. Many of the species which have these types of distribution in Ireland have ranges in Great Britain which do not extend into Scotland and, for reasons to be explained later (p. 356), probably were postglacial arrivals in both countries. But there are some whose ranges in Great Britain extend into Scotland and because of this the reasons for assuming a postglacial origin do not apply to them. These will be discussed here.

Schrankia costaestrigalis Stephens, *Abraxas sylvata* Scopoli (*ulmata* Fabricius), *Pseudopanthera macularia* L., *Drymonia ruficornis* Hufnagel (*chaonia* Schiffermüller) and *Thecla quercus* L. have southerly and westerly distributions in Ireland and have their headquarters in Great Britain in the south-west. Thus they may have been inhabitants of the glacial land south and west of the British Isles and it seems likely that they were second interstadial arrivals. *Apatele leporina* L. exhibits considerable local variation, apparently in the form of a cline. It, too, may date from the second interstadial. Evidence of relative antiquity is less obvious with *Amphipyra pyramidea* L., *Pyrrhia umbra* Hufnagel (*marginata* Fabricius), *Cosymbia punctaria* L., *Calothysanis amata* L. (*amataria* L.) and *Cossus cossus* L. (*ligniperda* Fabricius) (fig. 37), which also are species which have southerly distributions in Ireland but wide ranges in Great Britain. However, the fact that they have very local distributions in northern England and in Scotland may indicate some degree of relative antiquity. From analogy with the other species it seems not improbable that they were second interstadial phase arrivals.

Most, if not all, of these species probably were confined to the relatively temperate parts of southern England and of the glacial land south and west of the British Isles during the third glacial phase. But unlike the species discussed previously, they expanded their ranges and spread northwards to some extent in both Great Britain and Ireland in post-glacial times.

Finally there is a heterogeneous group of species which have been recorded from only one or two counties in Ireland (see Donovan, 1936) and do not fit into any of the above categories. Their origins are difficult to make out.

Of these, there is a possibility that *Cosmia affinis* L., *Hemerophila abruptaria* Thunberg and *Cleora ribeata* Clerck (*abietaria* Schiffermüller) have been artificially introduced into Ireland as their food-plants, elm, lilac and other garden shrubs, and conifers, respectively, have been imported in large quantities. If this was so then there is nothing to indicate that they were anything but postglacial arrivals in Great Britain. There is a possibility, however, that the last species may have survived since the first interstadial in the spruce forests where, presumably, *Thera variata* and *Eupithecia pusillata* survived.

Orthosia populi Stroem (*populeti* Fabricius) and *Zenobia subtusa* Schiffermüller, like *Sesia apiformis*, feed on *Populus*, and their very local distributions in Ireland and in Great Britain north of the Midlands may be due to the correspondingly local distributions of their food-plants. Possibly they invaded the British Isles with aspen in second interstadial times and invaded England again with the grey and black poplars in the postglacial. However, they are species knowledge of whose Irish distributions is particularly incomplete and until further information becomes available it is impossible to reconstruct their possible histories with any degree of confidence. The same applies to *Procus versicolor* Borkhausen, *Coenobia rufa* Haworth (*despecta* Treitschke), *Agrotis puta* Hübner, *Polia advena* Schiffermüller (*nitens* Haworth), *Amathes stigmatica* Hübner (*rhomboidea* Treitschke nec Esper), *Mesotype virgata* Hufnagel (*lineolata* Schiffermüller) and *Erannis leucophaea* Schiffermüller. These possibly date from the second interstadial, but it is at present difficult to date them satisfactorily. *A. puta* has a southerly distribution on the Continent and possibly invaded the British Isles during the postglacial climatic optimum, its present local distribution being due to its having undergone numerous local extinctions as a result of the climatic deterioration of the later postglacial. The same may apply to *H. abruptaria*, which also has a mainly southerly distribution abroad.

(c) *The Non-Irish Species.*

The species now to be discussed are the remainder which have not been found in Ireland, but for which there is some evidence to indicate that they may have inhabited Great Britain since Pleistocene times. In most cases, however, it is difficult to date them more definitely.

Eustroma reticulata Schiffermüller has been found only in the hill districts of north Wales and north-western England. This distribution may indicate that it becomes confined to the low-lying region between Ireland and Great Britain during the third glacial phase. Probably it dates at least from the second interstadial phase as an inhabitant of Great Britain. Its food-plant, yellow balsam (*Impatiens noli-metangere*), is regarded as being probably indigenous in the localities in

which the moth is found (Wilmott, *in litt.*). *Lampropteryx otregiata* Metcalfe is another species whose distribution indicates some degree of relative antiquity. It has been found only in damp woods in Devon and Cornwall, and this may indicate that it was an inhabitant of the glacial land south-west of England and therefore that it probably dates from an interstadial phase.

Next there are several species whose probable histories can be reconstructed mainly by analogy with species discussed previously.

Discoloxia blomeri Curtis (*pulchraria* Eversmann) has a very similar, westerly, type of distribution in Great Britain to *Abraxas sylvata* and has the same food-plant, wych elm (*Ulmus montana*). As the latter species probably dates from the second interstadial as an inhabitant of the British Isles (see p. 336) it seems likely that *D. blomeri* may have had a similar origin. The discontinuous distribution of *Chlorissa viridata* L. in Great Britain is very similar to that of *Sterrhia muricata* and there is thus a possibility that, like that species, it may date from the first interstadial phase.

Nonagria dissoluta Treitschke (*neurica* Duponchel nec Hübner) and *Hydrillula palustris* Hübner may have had histories similar to some of the Fenland species (p. 304), as they are confined to the fens of eastern England and exhibit some local variation there. Most British specimens of the former species apparently are referable to the form *arundineta* Schmidt, while about a third of the known British specimens of the latter are referable to the endemic form *lutescens* Farren. However, apart from saying that they probably were Pleistocene arrivals it is not possible to date them more definitely at present. Incidentally *H. palustris* may have arrived during a glacial, rather than an interstadial, phase as it now has a mainly northerly distribution on the Continent and a form very similar to *lutescens* occurs in Lapland (Tutt, 1902).

Heliothis maritima Graslin, which is found in the New Forest district, is represented in England by the ssp. *septentrionalis* Hoffmeyer, which has been found abroad in Denmark. Possibly it has had a similar history as a British species to *Eilema pygmaeola* (p. 304). That is, *septentrionalis* may have developed in a population which was isolated in the Dogger Land region for a time during the Pleistocene. However, the exact distribution of this species is not fully known, as until recently it was confused with the closely-allied *H. veriplaca*. It is therefore impossible to reconstruct its history with any degree of confidence at present. *Coscinia cribrum* L. (*cribraria* auctt.) is represented by two races in England, one, *arenaria* Lempke, on the coastal sandhills of the south-east, the other, *bivittata* South, on heaths in the New Forest district. The ssp. *arenaria* occurs also on the coastal sandhills of France, Belgium and Holland and may be a Dogger Land race which has had a history similar to *E. pygmaeola*, and thus may date from the Pleistocene. Alternatively, it may have become established in England in comparatively recent times by overseas migration from the Continent. The origin of the ssp. *bivittata* is not apparent; the variation may have developed in a colony which was isolated in the region of the English

Channel during the Pleistocene, or the race may be a postglacial arrival.

Finally there is a number of non-Irish species whose ranges in Great Britain extend from southern England at least to north of central Scotland. There are two main reasons for believing that they date from the Pleistocene. Firstly, as the species discussed in pp. 333-6—those which have wide ranges in Great Britain but very restricted ranges in Ireland—must have undergone numerous local extinctions in Ireland at some time in the past, it is reasonable that other species became wholly extinct in that country. The species under discussion may be examples of these. Secondly, and more importantly, there is a very large number of species (see pp. 352-5) whose ranges in Great Britain extend into central Scotland and for which there is not evidence to indicate that they were anything but postglacial arrivals in the British Isles. All of them have wide ranges in Ireland. If they are postglacial species then the species under discussion probably date from an earlier period.

The species in question include *Hepialus sylvinus* L. (fig. 38), *Cybosia mesomella* L., *Nola cuculatella* L., *Enargia paleacea* Esper (*fulvago* Hübner nec L.), *Dipterygia scabriuscula* L. (*pinastri* L.), *Anchoscelis litura* L., *Parastichtis ypsilon* Schiffermüller (*fissipuncta* Haworth), *Hadena genistae* Borkhausen (*w-latinum* Borkhausen), *Hypena rostralis* L. and *Aegeria culiciformis* L. With the apparent exception of *H. sylvinus* these all have very local distributions in northern England and in Scotland, which indicates some degree of relative antiquity. Their most probable history is that they spread over the British Isles in second interstadial times and became extinct in Ireland during the third glacial phase. The occurrence of *H. rostralis* in the Isle of Rhum indicates that it was an inhabitant of the glacial land west of Scotland. There is a possibility that some may have been glacial, rather than interstadial, phase arrivals, dating perhaps from the second glacial phase. Possible examples are *A. litura*, which is perhaps more frequent in Scotland than in southern England, *C. mesomella*, which inhabits heathy situations, and *H. sylvinus* and *P. ypsilon*, which have northern and central European distributions abroad.

There is a number of other non-Irish species whose ranges in Great Britain appear to extend into central Scotland, but it would seem that they have been recorded from localities north of the Clyde on only one or two occasions and there are reasons for believing that some of the Scottish records may be erroneous. Pending confirmation of the records from central and northern Scotland such species may be regarded as not occurring as natives north of the Clyde and are included in Chapter IX.

(d) Further Pleistocene Arrivals.

There are several species not discussed previously whose distributions indicate that they may be relatively ancient inhabitants of the British Isles. They have mainly southerly and westerly distributions, which might indicate that they were inhabitants of the glacial land south and west of the British Isles. Of course, in some cases their

distributions may be regulated by existing climatic conditions, but this seems less probable. The chief characteristics of the climate of the south-western and western districts of the British Isles are that the winter temperatures and annual rainfalls are relatively high in comparison with those of the eastern districts of Great Britain. The first of these factors is unlikely to be of any great importance to the species in question as with two exceptions (*Perconia strigillaria* Hübner and *Acasis viretata* Hübner) they all inhabit northern Europe, the majority of them having northern and central European distributions. There is no apparent evidence that any of the species requires a high humidity or a high rainfall, although this factor may be of some importance with *Eustrotia uncula* Clerck, *Eupithecia valerianata* Hübner and *P. strigillaria*, which inhabit boggy or marshy situations, and with the lichen-feeding *Nudaria mundana* L. *Lithophane socia* Hufnagel (*petrificata* Schiffermüller) may have its distribution regulated mainly by that of its food-plant, ash, but as it exhibits local variation in the British Isles it may have had a history similar to such ash-feeding species as *Craniophora ligustri* and *Eupithecia innotata* ssp. *fraxinata*. It it had, then, unlike those two species, it spread over the whole of Ireland in postglacial times from the region to which it had been confined during the third glacial phase. The occurrence of *H. uncula* in the Isle of Rhum, an island which probably was not connected to the Scottish mainland by land in postglacial times, indicates that it was a Pleistocene arrival and the probability is that all these species, together with *Eupithecia virgaureata* Doubleday, *E. distinctaria* Herrich-Schäffer (*constrictata* Guenée), *Asthenia albulata* Hübner (*candidata* Schiffermüller), *Anagoga pulveraria* L. and *Pararge aegeria* L. (fig. 39), which also have wide ranges in the British Isles but tend to be most frequent in the south-western or western districts, date from the second interstadial, but some may have arrived at earlier dates.

Then there are species whose relative antiquity is indicated only or mainly by taxonomic evidence. Of these the following are represented by distinct subspecies in the British Isles: *Arctia villica* L. ssp. *britannica* Oberthur, *Pachetra sagittigera* Hufnagel (*leucophaea* Schiffermüller) ssp. *britannica* Turner and *Zygaena meliloti* Esper ssp. *anglica* Reiss, which are confined to Southern England, and *Bena prasinana* L. ssp. *britannica* Turner, *Euplexia lucipara* L. ssp. *britannica* Turner, *Hadena serena* Schiffermüller ssp. *leuconota* Eversmann, *Eupithecia icterata* de Villers ssp. *subfulvata* Haworth and *Perizoma albulata* Schiffermüller ssp. *griseata* Staudinger, whose ranges cover all or most of the British Isles. The variation of these species indicates that they are relatively ancient inhabitants of the British Isles and it is probable that they date from an interstadial phase, perhaps from the first. That *P. albulata*, at least, probably dates from the first interstadial is indicated by its occurrence in the Faroes. Unlike most interstadial survivors, these must have spread in postglacial times from the areas to which they had been confined during the glacial phases, just as did *Hadena lepida* ssp. *capsophila* and *Maniola jurtina* ssp. *iernes*.

Many of the species whose ranges cover most or all of the British

Isles exhibit variation which may indicate some degree of relative antiquity. Those which exhibit variation in the form of clines may, in many cases, date from the Pleistocene, but apart from their variation there is little to indicate that they were anything but postglacial arrivals in the British Isles. As a matter of opinion, however, it would seem likely that they date from the Pleistocene. The species in question are each represented by one race in Ireland and Scotland which grades into the typical race found in southern England. The following are some examples of northern and western races: *Phragmatobia fuliginosa* L. race *borealis* Staudinger, *Rusina umbratica* Goeze (*tenebrosa* Hübner) race *obscura* Tutt, *Meristis trigrammica* Hufnagel (*trilinea* Hübner) race *bilinea* Haworth, *Xylophasia hepatica* Hübner race *characterica* Hübner, *Agrochola lota* Clerck race *rufa* Tutt, *A. macilenta* Hübner race *obsoleta* Tutt, *Eupsilia transversa* Hufnagel (*satellitica* L.) race *rufescens* Tutt, *Bombycia viminalis* Fabricius race *obscura* Staudinger, *Leucania lythargyria* Esper reddish race, *Polia nebulosa* Hufnagel race *pallida* Tutt and *Notodonata dromedarius* L. race *perfusca* Buchanan-White. There is a possibility that some of these races may be distinct subspecies, rather than stages in clines, as their status often is not made clear in the literature. If so, then they may represent invasions distinct from the typical races, the latter probably being postglacial arrivals.

Many other species are represented by local races or develop local forms in parts of their ranges in the British Isles. It is possible that some of these races may represent the survivors of Pleistocene invasions, the typical forms of the species representing postglacial invasions. However, as with the species listed in the last paragraph, the probable histories of these are difficult to reconstruct at present. Examples of such local races or forms are the race *curtisii* Newman of *Triphaena comes* Hübner (*orbona* Fabricius nec Hübner), the races *orcadensis* Staudinger and *hebridensis* Parkinson-Curtis of *Eupithecia venosata* Fabricius, the race *cinereae* Gregson, of *E. tenuata* Hübner, the race *plumbata* Curtis of *Plemyria bicolorata* Hübner, the race *albocrenata* Curtis of *Electrophaes corylata* Thunberg, the race *appimaria* Weaver of *Oporinia dilutata* Schiffermüller and the races *conversaria* Hübner and *sodorensium* Weir of *Cleora repandata* L. Most of these races are confined to isolated and remote parts of the mountains or islands of Scotland.

(e) *The Lepidoptera of the Shetlands and Hebrides.*

It is likely that the Shetlands have been islands since before the end of the Pleistocene, as they are at present separated from the mainland by depths of more than 40 fathoms, while there is no evidence that the sea was ever more than about 30 fathoms below its present level around the British Isles in postglacial times. It is apparent, therefore, that all the non-migratory species of Lepidoptera now inhabiting the Shetlands must have become established there before the end of the Pleistocene. This is further indicated by the composition of the Shetlandic lepidopterous fauna. Of the 51 non-migratory species of Macrolepidoptera

which have been reliably recorded from the Shetlands (see Beirne, 1945) no less than 37 show evidence other than their occurrence in the Shetlands of being of Pleistocene age as inhabitants of the British Isles. The remaining 14 species probably invaded the British Isles both in Pleistocene and in postglacial times and are wholly of Pleistocene age as inhabitants of the Shetlands. Elsewhere in the British Isles the Pleistocene survivors were overwhelmed by interbreeding with the postglacial arrivals so that little or no trace of them now exists. The fourteen species are as follows: *Hepialus humuli* L., *H. lupulinus* L., *Caradrina clavipalpis* Scopoli (*quadripunctata* Fabricius), *Apamea sordens* Hufnagel (*basilinea* Schiffermüller), *Xylophasia remissa* Hübner (*obscura* Haworth, *gemina* Hübner), *Hydraecia micacea* Esper, *Procus fasciunculus* Haworth, *Leucania pallens* L., *Orthosia gothica* L., *Diataraxia oleracea* L. (*essoni* Hampson), *Hada nana* Hufnagel (*dentina* Schiffermüller), *Chloroclystis miata* L., *Xanthorhoe fluctuata* L. and *Calostigia didymata* L. That the Shetlandic populations are relatively ancient inhabitants in comparison with the populations found elsewhere in the British Isles is further indicated by some of these species being represented by endemic local races in the Shetlands, examples being *H. humuli*, *P. fasciunculus*, *H. nana* and *X. didymata*. Even some of the suspected migrants, for example *Xanthorhoe montanata* and *Euphyia bilineata*, develop local forms there, a fact which indicates that, with these two species at least, overseas migration to the Shetlands has been negligible.

Because of the isostatic sinking of the land in the north during the third glacial phase it seems unlikely that the Shetlands could have been connected to the Scottish mainland by land at that time. Thus the Shetlandic Lepidoptera probably date from the second interstadial phase at the latest. There is evidence that some of them date from not later than the first interstadial. This is provided by their occurrence in the Faroes and, in two cases at least, by there being a taxonomic resemblance between the Shetlandic and Faroese races. Thus, the form *thulensis* Newman of *H. humuli* is found only in the Shetlands and Faroes, being dominant in the former islands and frequent in the latter, and female *Xanthorhoe designata* from the Faroes tend to resemble the Shetlandic race (Wolff, 1929). *H. nana* is another species not discussed in previous chapters which occurs in both the Shetlands and Faroes. Finally, many of the species found in the Shetlands are wholly of first glacial or second interstadial age as inhabitants of the British Isles.

The composition of the Lepidopterous fauna of St. Kilda indicates that it probably is wholly of Pleistocene age. Furthermore, because of depths of sea separating it from the Scottish mainland it is unlikely that St. Kilda was connected to the Scottish mainland by land later than the second interstadial phase. Most of the non-migratory inhabitants of St. Kilda have been mentioned previously and further species are *Hadena thalassina* Hufnagel, *Orthosia incerta* Hufnagel (*instabilis* Schiffermüller) and *Anaitis plagiata* L., for which there is no good evidence to indicate that they were anything but postglacial arrivals elsewhere in the British Isles. As with the Shetlandic species listed above, these

probably spread over the British Isles, including St. Kilda, in Pleistocene times and again in the postglacial, the latter invasion not reaching St. Kilda. To these may be added *Procus fasciunculus*, whose Pleistocene age is indicated also by its occurrence in the Shetlands, and *Eupithecia venosata*, whose variation indicates that it invaded the British Isles in Pleistocene, as well as postglacial, times. The lepidopterous fauna of St. Kilda is imperfectly known (Corbet, 1945) and the occurrence of such species as *Sterrhia rusticata* there indicates that it would repay investigation.

On the distribution and variation of the Lepidoptera the Hebrides may be divided into two groups (Harrison), one including the Outer Isles and Canna, Rhum, Eigg, Muck, Coll and Tiree, the second including the remaining Inner Isles. In the first group are found many species which are of Pleistocene age as inhabitants of the British Isles, while many of the postglacial invaders are absent although found in the islands of the second group.

The reason why many Pleistocene species have their headquarters in the Outer Isles or in the Rhum and Coll groups is that these islands were not ice-covered during the third glacial phase, while most of the remaining Inner Hebrides and the greater part of the adjacent Scottish mainland was under the Highland ice-sheet (see fig. 1). Good examples of species which survived the third glacial phase on the ice-free land west of the Highland ice-sheet are *Setina irrorella*, *Eustrotia uncula*, *Hypena rostralis*, *Nyssia zonaria*, *Tethea fluctuosa*, *Maculinea arion*, *Phothedes captiuncula*, *Zygaena purpuralis* and *Z. achilleae*, as well as the ssp. *splendida* of *Maniola jurtina*, the ssp. *insularum* of *Argynnis selene* and the ssp. *praeclara* of *Euphydryas aurinia*. The reason why many of the postglacial species which occur in the Inner Hebrides and on the Scottish mainland are absent from or relatively rare in the Outer Hebrides and the Rhum and Coll groups is that those islands probably were not connected to the mainland by land in postglacial times. It is significant that they are all separated from the mainland by depths of more than 30 fathoms. This indicates that they must have become isolated by the rising sea long before the remaining Inner Isles, all of which are separated from the mainland by depths of less than 30 fathoms. Probably the latter were connected to the mainland in early postglacial times, when the sea was up to 30 fathoms below its present level, while the Outer Hebrides and the Rhum and Coll groups were not.

A much larger number of species for which there is otherwise no indication of a Pleistocene origin occur in the Outer Isles and the Rhum and Coll groups than occur in the Shetlands. Most of them may be species which spread over the British Isles in Pleistocene times and again in the postglacial and which survived the third glacial phase in the Hebrides but became extinct in the Shetlands. Their survival in the Hebrides may have been due partly to the larger areas of land available and partly to the milder climates as compared with the Shetlands. But in many cases the species may have invaded these Hebridean islands in the postglacial despite the absence of land-connections. When the postglacial sea-level was at its lowest around western Scotland these

islands must have been separated from the Scottish mainland only by relatively narrow straits over which many species could have flown.

An excellent example of such a species is *Maniola jurtina*. In late glacial times it probably was represented by its ssp. *splendida* throughout the Hebrides and western Scotland, but the postglacial invaders, represented by the typical subspecies, overwhelmed it by interbreeding with it on the Scottish mainland and in the Inner Hebrides, except in a few localities where colonies were isolated by the mountains and still survive. The typical subspecies then spread into the Rhum and Coll groups by overseas flight—the species is one which is known to undertake such flights—and overwhelmed *splendida* there also. It also reached the Outer Isles, probably spreading from Skye to Lewis, but has not arrived in sufficient numbers to overwhelm *splendida* throughout those islands. That subspecies still survives in the most southerly of the Outer Isles—in the islands which were most remote from the mainland in early postglacial times and to which the typical subspecies has not yet spread.

The islands under discussion probably have been isolated from each other as well as from the mainland in postglacial times. Judging from the present depths of sea, Coll and Tiree must have been connected to each other in the early postglacial, and therefore they should support very similar lepidopterous fauna. The same applies to Eigg and Muck. The faunas of these two groups should differ from each other and from those of Rhum, of Canna and of the Outer Isles to some extent, and the last three faunas also should differ from each other. Professor J. W. Heslop Harrison's records indicate that there are in fact considerable differences between the lepidopterous faunas of these different groups, both in their compositions and in the relative abundance of different species.

The reason why so many Pleistocene survivors are found in Rhum may be that because of the height to which it rises above sea-level (over 1,500 feet) it must have been little affected by the isostatic sinking of the Hebrides during the third glacial phase, while Coll and Tiree, for example, must have been largely submerged at that time.

IX. THE POSTGLACIAL ARRIVALS.

(a) *Postglacial Climatic and Vegetational Changes.*

The Pleistocene period is regarded as having ended some 22,000 years ago,¹⁰ the subsequent period being known as the postglacial or Holocene. It is divided into a number of climatic periods, of which the first was the Pre-Boreal. During the Pre-Boreal period the climate of the British Isles was colder than at present but was gradually becoming warmer. Remnants of the last ice-sheets were still present in Scotland and the greater part of the British Isles was covered with open woodland in which Birch was the dominant tree. It was succeeded by the Boreal period, when the climate became warmer, dryer and more continental. There was a general extension of forest, pine replacing birch as the

¹⁰ Zeuner's estimate ; most writers give much lower estimates.

dominant tree and other trees increasing. Up to the end of this period the sea-level was lower than now, the coast-line probably coinciding roughly with the present 30-fathom line. The southern part of the North Sea was dry land—the “Dogger Land”—connecting England to the Continent. But the sea-level was rising and during the following climatic period, the Atlantic period, it rose sufficiently to cover the Dogger Land and to sever England from the Continent. This took place less than 8,000 years ago. The Atlantic climate was warmer, wetter and more oceanic than that of the Boreal, and for a time was rather warmer than that of the present day. Dense forests covered most of the British Isles. Pine decreased but there was a considerable increase of oak and other deciduous trees.

It is apparent that Lepidoptera characteristic of all types of climate from cold to warm temperate and from dry and continental to damp and oceanic could have invaded the British Isles in postglacial times before the severance of the British-European land-connection. The postglacial saw the arrival of the largest number of species since first interstadial times and these postglacial arrivals are now the dominant species over most of the British Isles.

The Atlantic period was succeeded by the Sub-Boreal, when the climate became somewhat dryer and more continental and as a result there was some increase of pine. There is no definite line of demarcation between these two periods. During the following, the Sub-Atlantic, period the climate became colder, wetter and more oceanic, particularly in the north, and has continued like that up to the present day. During this period the vegetation of the British Isles was drastically modified by man. The dense forests which covered the British Isles from sea-level up to 1,000 feet on the hills have been so greatly cleared that at present less than 5 per cent. of the country is wooded and only a small proportion of this represents the remnants of the natural woodland, the larger part being wholly or mainly planted or otherwise modified by man. Numerous local extinctions of the woodland Lepidoptera must have resulted and it would not be an exaggeration to say that 4,000 years ago the woodland species occurred in areas covering up to twenty times the areas of their present distributions. However, the ranges of the majority probably have been little affected, as the surviving remnants of the native forests are sufficiently numerous and widespread to have enabled each species to have survived in one or more localities in each part of its original range. The reclamation of fens, marshes, bogs, heaths, and moors has affected the distributions of most of the species characteristic of these types of habitat, but to a lesser degree than the woodland species. The enormous increase of grassland and cultivated land has resulted in corresponding increases in the distributions of the Lepidoptera characteristic of grasslands and of hedgerows. In Prehistoric times these species must have inhabited the glades and margins, respectively, of the forests. Finally, in comparatively recent times, a number of species have been added to the British fauna or have been established in localities in which they did not occur as natives by deliberate or accidental importations (see p. 278).

Because of the position of the land-connection to the Continent the postglacial invaders must have spread firstly into southern and eastern England and then northwards and westwards (fig. 45), until they reached regions where ecological conditions were unfavourable to them. The majority have not expanded or reduced their ranges to any important extent since, as the climatic changes of the later postglacial were slight



FIGS. 40-44.—Types of ranges of post-glacial Lepidoptera.

FIG. 45.—Directions of spread over the British Isles of the post-glacial arrivals.

in comparison with those endured by the Pleistocene arrivals. Lepidoptera whose ranges and distributions indicate that they invaded England from the south-east and spread northwards and westwards in Great Britain, for which no evidence of greater antiquity is indicated by their ecology, by their variation or by their distributions in Ireland, and whose ranges and distributions appear to be regulated primarily by existing ecological conditions and not by conditions which no longer exist, may be regarded as having been postglacial arrivals. It is, of course, quite

possible that many of them date from the Pleistocene, but in the absence of any evidence it is impossible to say which they are.

A large proportion of these presumed postglacial arrivals are found in Ireland, where none has a range or distribution which would indicate any greater degree of antiquity. This is sufficient evidence for the existence of a postglacial land-connection between Ireland and Great Britain. Those who have studied the Irish fauna and flora are in agreement that such a land-connection must have existed, but there is controversy as to its position. The ranges of the Lepidoptera provide strong evidence of the site of this former land-connection. This evidence is best explained by considering the postglacial species in two sections: the species which do not occur in Ireland and those which do.

(b) *The Non-Irish Species.*

First there are species which are confined to limited areas in the south or south-east of England:—

<i>Nola albula</i> Schiffermüller	<i>Colobochyla salicalis</i> Schiffermüller.
<i>Roeselia aerugula</i> Hübner (<i>centonalis</i> Hübner).	<i>Laelia coenosa</i> Hübner.
<i>Apatele auricoma</i> Schiffermüller.	<i>Scopula nigropunctata</i> Hufnagel (<i>strigillaria</i> Hübner, <i>prataria</i> Boisduval).
<i>Acosmetia caliginosa</i> Hübner.	<i>S. immorata</i> L.
<i>Nonagria neurica</i> Hübner (<i>edelsteni</i> Tutt).	<i>Lithostege griseata</i> Schiffermüller.
<i>Hapalotis venustula</i> Hübner.	<i>Coenotephria berberata</i> Schiffermüller.
<i>Arenostola extrema</i> Hübner (<i>concolor</i> Guenée).	<i>Cleora arenaria</i> Hufnagel (<i>angularia</i> Thunberg, <i>viduaria</i> Schiffermüller).
<i>Sedina büttneri</i> Hering.	<i>Bapta pictaria</i> Curtis (<i>distinctata</i> Herrich-Schaffer).
<i>Heliothis veriplaca</i> Hufnagel (<i>dipsacea</i> L.).	<i>Pygaera anachoreta</i> Schiffermüller.
<i>Cirrhia ocellaris</i> Borkhausen.	<i>Drepana harpagula</i> Esper (<i>hamula</i> Schiffermüller).
<i>Cucullia gnaphalii</i> Hübner.	<i>Procris globulariae</i> Hübner.
<i>Trigonophora flammea</i> Esper (<i>empyrea</i> Hübner).	<i>Phragmatoecia castaneae</i> Hübner (<i>arundinis</i> Hübner).
<i>Senta flammea</i> Curtis.	<i>Aegeria chrysidiformis</i> Esper.
<i>Anepia irregularis</i> Hufnagel (<i>echii</i> Borkhausen).	<i>Sciapteron tabaniformis</i> von Rotenburg (<i>vespiformis</i> Westwood nec L.).
<i>Hadena albimacula</i> Borkhausen.	
<i>Paracolax derivalis</i> Hübner.	

Of these, the range of *A. irregularis* is regulated by that of its food-plant, *Silene otites*. It is confined to the Breck district of East Anglia, as in the day-flying and sun-loving *H. veriplaca*, whose distribution, however, may be due to that district having the most continental climate of any part of the British Isles, the dryness of the summers being accentuated by the sandy soil. There is a possibility that *D. harpagula* may have its range limited by the occurrence of the small-leaved lime (*Tilia cordata*) as a native tree. This appears to be its sole food-plant in

England, but on the Continent it attacks also birch, oak and beech. No explanation for its preference for lime in England can be offered.

A larger number of species have wider ranges but are confined to the south or south and east of England, not occurring north of Yorkshire or south Lancashire (fig. 40). They are as follows :—

- Pelusia muscerda* Hufnagel.
Eilema griseola Hübner.
Panaxia dominula L.
Nola strigula Schiffermüller.
Pseudoips bicolorana Fuessley (*quercana* Schiffermüller).
Simyra albovenosa Goetze.
Nonagria geminipuncta Hatchett.
N. cannae Ochseneiner (*algae* Esper nec Fabricius).
Chilodes maritima Tauscher (*ulvae* Hübner).
Cosmia pyralina Schiffermüller.
C. diffinis L.
Zenobia retusa L.
Dicycla oo L.
Arenostola fluxa Treitschke (*helfmannii* Eversmann).
Oria musculosa Hübner.
Trachea atriplicis L.
Eremobia ochroleuca Schiffermüller.
Jodia croceago Schiffermüller.
Tiliacea aurago Schiffermüller.
Cucullia lychnitis Rambur.
Lithophane semibrunnea Haworth.
Leucania obsoleta Hübner.
Hadena dysodea Schiffermüller (*chrysozona* Borkhausen).
Xylomiges conspiciellaris L.
Zanclognatha cribrumalis Haworth (*cribralis* auctt.).
Trisateles emortualis Schiffermüller.
Schrankia taenialis Hübner (*albistrigalis* Haworth).
Laspeyria flexula Schiffermüller.
Ophiura pastinum Treitschke.
Catocala sponsa L.
C. promissa Schiffermüller.
Acontia luctuosa Schiffermüller.
Plusia chryson Esper.
Orgyia gonostigma Fabricius (*recens* Hübner).
Euproctis phaeorrhoea Donovan (*chrysorrhoea* Hübner nec L.).
Sterrhia emarginata L.
Cosymbia orbicularia Hübner.
C. trilinearia Borkhausen (*linearia* Hübner) (see p. 279).
C. annulata Schulze (*omicronaria* Schiffermüller).
Hemistola immaculata Thunberg (*vernaria* Hübner, *chrysoprasaria* Esper) (see p. 279).
Comibaena pustulata Hufnagel (*bajularia* Schiffermüller).
Eupithecia isogrammaria Herrich-Schäffer (*haworthiata* Stainton) (see p. 279).
E. inturbata Hübner (*subciliata* Guenée).
E. irriguata Hübner.
E. insigniata Hübner (*consignata* Borkhausen).
Horisme vitalbata Schiffermüller.
H. tersata Schiffermüller.
Anticollis sparsata Treitschke (*sparsaria* Hübner).
Anaitis efformata Guenée.
Coenoteophria sagittata Fabricius.
Melanthia procollata Schiffermüller.
Minoa murinata Scopoli (*euphorbiata* Schiffermüller).
Xanthorhoe quadrifasciata Clerck.
Ortholitha umbrifera Prout.
Brephos notha Hübner.
Semiothisa alternata Schiffermüller (*alternaria* Hübner).
Ectropis luridata Borkhausen (*extersaria* Hübner).
Boarmia roboraria Schiffermüller.
Pachygnemina hippocastanaria Hübner (see p. 331).
Siona lineata Scopoli (*dealbata* L.).
Tethea octogesima Hübner (*ocularis* Guenée).
Hemaris fuciformis L.
Dilina tiliae L.
Ptilophora plumigera Schiffermüller (fig. 40).
Lophopteryx cucullina Schiffermüller (*cuculla* Esper).
Limenitis camilla L. (*sibilla* L.).

Apatura iris L.
Lysandra coridon Poda.
L. bellargus Rottenburg (*adonis* Hübner).
Strymonidia pruni L.
Aporia crataegi L.
Hesperia comma L.
Drepana cultraria Fabricius (*un-
 guicula* Hübner).
Heterogenea asella Schiffermüller
 (*cruciata* Knoch).

Apoda avellana L. (*limacodes* Hufnagel, *testudo* Schiffermüller).
Zeuzera pyrina L. (*aesculi* L.).
Aegeria myopaeformis Borkhausen.
A. flaviventris Staudinger.
A. andreniformis Laspeyres (*allanti-
 formis* Newman).
A. spheciiformis Schiffermüller.
Dipsosphesia scopigera Scopoli
 (*ichneumoniformis* Fabricius).

The ranges of many of these species are determined by the occurrence of their food-plants as natives. Examples are the beech-feeding *C. trilinearia*, *D. cultraria*, *H. asella* and *A. avellana*, the clematis-feeding *E. isogrammaria*, *H. vitalbata*, *H. tersata* and *M. procellata*, the lime-feeding *D. tiliae*, *T. aurago* which feeds on maple, beech, and sycamore, and *C. annulata*, *E. inturbata*, *P. plumigera* and *L. cucullina* which feed on maple and sycamore. Climatic factors probably regulate the ranges of others (see below).

To the above list may be added the following races mentioned in earlier Chapters: *Eumichtis lichenea* ssp. *lichenea*, *Eupithecia denotata* ssp. *denotata*, *Hydrelia flammeolaria* maple-feeding race, *Plebejus argus* ssp. *argus*, *Aricia agestis* ssp. *agestis* and *Lasiocampa quercus* ssp. *quercus*.

The following are the non-Irish species whose ranges extend into northern England but apparently not north of the Southern Uplands of Scotland (fig. 41).

Spilosoma urticae Esper (*papyrata* Marsh).
Diptera alpium Osbeck (*orion* Esper).
Xylophasia scolopacina Esper.
Apamea pabulatricula Brahm (*con-
 nexa* Borkhausen).
Hydraecia petasitis Doubleday.
Procus latrunculus Schiffermüller.
Gypsites leucographa Schiffermüller.
Tiliacea citrago L.
Antitype flavicincta Schiffermüller.
Catocala nupta L.
Scopula ornata Scopoli.
Eupithecia linariata Schiffermüller.
Calocalpe cervinalis Scopoli (*certata* Hübner).
Philereme transversata Hufnagel
 (*rhannata* Schiffermüller).
Euchoeca obliterata Hufnagel (*nebu-
 lata* Hübner).
Apocheima hispidaria Schiffermüller

Crocota ochrearia Rossi (*citraria* Hübner).
Selenia tetralunaria Hufnagel (*illus-
 traria* Hübner).
Deuteronomos fuscantaria Haworth.
Polyplaca ridens Fabricius.
Melanargia galathea L.
Argynnis cydippe L. (*adippe* auctt.).
Nymphalis polychloros L.
Polygonia c-album L.
Hamearis lucina L.
Strymonidia w-album Knoch (fig. 41).
Pyrgus malvae L.
Thymelicus sylvestris Poda (*flavus* Brünnich, *thauamas* Hufnagel).
Drepana binaria Hufnagel (*hamula* Schiffermüller).
Zygaena trifolii Esper.
Procris geryon Hübner.
Aegeria vespiformis L. (*asiliiformis* von Rottenburg, *cynipiformis* Esper).

To which may be added *Leucania impura* ssp. *impura*, *Hadena lepida* ssp. *lepida*, *Ceramica pisi* ssp. *pisi*, *Plemyria bicolorata* race *bicolorata*, *Electrophaes corylata* race *corylata*, *Tethea* or race or and *Trichiura crataegi* ssp. *crataegi*.

Some of these species have their ranges determined by the occurrence of their food-plants as natives, examples being the lime-feeding *T. citrigo* and the buckthorn-feeding *P. transversata*.

Finally there is a comparatively small number of non-Irish species whose ranges in Great Britain extend north of the Southern Uplands. Most of them have not been recorded reliably from north of the Scottish Lowlands or of Clydesdale. *H. paludis* and *S. virgularia* have been recorded from farther north, but there is a possibility that the records may be incorrect or, alternatively, that the species occur in Ireland but have been overlooked there. The reason for this is that each is easily confused with allied species and thus is likely to be overlooked or certain of its allies are liable to be mistaken for it. The species in question are as follows :

Spaelotis ravida Schiffermüller.
(*obscura* Brahm).

Mythimna turca L.

Sterrha virgularia Hufnagel (*incanaria* Hübner, *seriata* Schrank).

S. fuscovenosa Goeze (*interjectaria* Boisduval).

S. trigeminata Haworth.

Cosymbia porata Fabricius.

Trichopteryx polycommata Schiffermüller.

Euphyia rubidata Schiffermüller.

Ortholitha bipunctaria Schiffermüller.

Asphalia diluta Schiffermüller.

Sphinx ligustri L.

Notodonta anceps Goeze (*trepida* Esper).

Ochlodes venata Bremer and Grey
(*syllvanus* Esper nec Drury).

To which may be added *Ectropis bistortata* ssp. *bistortata*, *Maniola jurtina* ssp. *jurtina*, *Argynnis selene* ssp. *selene*, *Euphydryas aurinia* ssp. *aurinia* and *Polyommatus icarus* ssp. *icarus*.

Two of the above species have their ranges determined by that of their food-plant : the privet-feeding *T. polycommata* and *S. ligustri*.

While some of the species given in the above lists have their ranges determined by the ranges of their food-plants, climatic conditions probably limit the ranges of the majority. The south of England is the warmest, driest and sunniest part of the British Isles and it is significant that almost half of the day-flying and sun-loving species of Lepidoptera are confined to that region. In Great Britain both the annual and the summer temperatures decrease from south to north and one or both of these may be important with the majority of the species. Most probably, however, it is the amount of heat during certain stages of the life-cycle—particularly during the larval and imaginal stages—that is important in determining the ranges in most cases. As different species are in the larval and imaginal stages at different times of the year and for different lengths of time it is impossible to make any generalisations on this point.

Many species are confined to the chalk downs of southern England,

but in no case is there any evidence that this is due directly to the composition of the soil. In most cases the soil affects the distributions indirectly : the species feed on plants which grow only or mainly on the chalk. In some instances ecoclimatic conditions may be of importance : the extreme dryness of the shallow and well-drained soil of the chalk downs. And in some instances the occurrence of species only or mainly on the chalk may be a mere coincidence between the species' ranges and the distribution of chalk. In the British Isles chalky formations are confined to the south and east of England, and if a species is confined to that region by ecological factors other than the indirect effects of the nature of the soil and if it inhabits open pastures, then it will tend to occur only or mainly on the chalk downs.

(c) *The Irish Species.*

Of the presumed postglacial arrivals no species which is confined to a relatively limited area in the south or east of England (as are the species given in the first list of section (b)) is found in Ireland. Only a small proportion of both the species whose ranges cover most of Great Britain south of Yorkshire and south Lancashire and whose ranges extend into northern England but not north of the Southern Uplands of Scotland are found there.

The majority of the Irish species whose ranges in Great Britain do not extend north of the Southern Uplands of Scotland are confined to the southern half of Ireland, or at least are widely distributed in the southern half of the country but are very local in the north. The reasons for their Irish distributions will be discussed later (p. 356). Of these, the following are species whose ranges in England do not extend north of Yorkshire :

<i>Apatele alni</i> L.	<i>Orthosia miniosa</i> Schiffermüller.
<i>Triphaena interjecta</i> Hübner.	<i>Dasychira pudibunda</i> L.
<i>Dasyampa rubiginea</i> Schiffermüller.	<i>Eupithecia trisignaria</i> Herrich-Schäffer.
<i>Leucania pudorina</i> Schiffermüller (<i>impudens</i> Hübner).	<i>Euphyia picata</i> Hübner.
<i>Maniola tithonus</i> L. (fig. 43).	<i>Aegeria formicaeformis</i> Esper.
<i>Leucania straminea</i> Treitschke.	

And the following have ranges which extend into northern England but not north of the Southern Uplands :

<i>Brachionycha sphinx</i> Hufnagel (<i>castanea</i> Schiffermüller).	<i>Hydrelia sylvata</i> Schiffermüller (<i>testacea</i> Donovan).
<i>Sterrhia subsericeata</i> Haworth.	<i>Hygrochroa syringaria</i> L.
<i>Scopula immutata</i> L.	

Two of the species whose ranges in Great Britain extend farther north have southerly distributions in Ireland : *Atolmis rubricollis* L. and *Phytometra viridaria* Clerck (*aenea* Hübner).

Then there are some species which are confined to the northern half of Ireland or are widely distributed in the north but very local in the south. They include a single species whose range in Great Britain does not extend north of Yorkshire : *Cerura hermelina* Goeze (*bifida* Brahm.) (fig. 42) ; two whose ranges do not extend north of the Southern Uplands : *Hydraecia ophiogramma* Esper and *Zygaena lonicerae* von Scheven ; and thirteen whose ranges in Great Britain extend at least as far north as the Clyde :

Petilampa minima Haworth (*arcuosa* Haworth).
Apamea unanimitis Hübner.
Orthosia munda Schiffermüller.
Episema caeruleocephala L.
Eupithecia expallidata Guenée.
Cidaria fulvata Förster.
Ecliptopera silaceata Schiffermüller.

Triphosia dubitata L.
Perizoma affinitata Stephens.
P. flavofasciata Thunberg (*decorata* Hübner).
Xanthorhoe ferrugata Clerck (*undentaria* Haworth).
Odezia atrata L. (*chaerophyllata* L.).
Erannis aurantiaria Esper.

The reasons why these species have southerly or northerly distributions in Ireland will be discussed later (p. 356).

The majority of the postglacial arrivals have ranges which cover the whole of Ireland. Of these, however, there are only two species whose ranges in Great Britain do not extend north of Yorkshire : *Eilema complana* L. and *E. lurideola* Zincken ; and only seven whose ranges extend into northern England but not north of the Southern Uplands : *Conistria ligula* Esper (*subspadicea* Staudinger, *spadicea* Haworth nec Hübner), *Chloroclystis coronata* Geyer, *Eupithecia dodoneata* Guenée, *Euphyia unangulata* Haworth, *Biston strataria* Hufnagel (*prodromaria* Schiffermüller), *Argynnis paphia* L. and *Celastrina argiolus* L. The great majority have ranges in Great Britain which extend at least as far north as the Clyde and in most cases north of the central Highlands ; they are as follows :

Arctia caja L.
Roeselia confusalis Herrich-Schäffer.
Sarothripus revayana Scopoli (*undulana* Hübner nec Schiffermüller).
Apatele tridens Schiffermüller.
A. psi L.
A. megacephala Schiffermüller.
A. rumicis L.
Calocasia coryli L.
Cryphia perla Schiffermüller.
Gortyna flavago Schiffermüller (*ochracea* Hübner).
Nonagria typhae Thunberg (*arundinis* Fabricius).
Caradrina clavipalpis Scopoli (*quadripunctata* Fabricius) (see p. 342).
C. morpheus Hufnagel.

C. blanda Schiffermüller (*superstes* Ochsenheimer).
C. alsines Brahm.
Mormo maura L.
Thalpothila matura Hufnagel (*cytherea* Fabricius).
Xylophasia remissa Hübner (*obscura* Haworth, *gemina* Hübner) (see p. 342).
X. crenata Hufnagel (*rurea* Fabricius).
X. lithoxylea Schiffermüller.
X. sublustris Esper.
Apamea sordens Hufnagel (*basilinea* Schiffermüller) (see p. 342).
Hydraecia micacea Esper (see p. 342).
H. oblonga Haworth (*abjecta* Hübner).

- H. oculea* L. (*nictitans* Borkhausen nec L.).
Procus fasciunculus Haworth (see p. 342).
P. strigilis Clerck.
Ochropleura plecta L.
Graphiphora augur Fabricius.
Amathes triangulum Hufnagel.
A. umbrosa Hübner (*sexstrigata* Haworth).
A. baja Schiffermüller.
Diarsia brunnea Schiffermüller.
Triphaena janthina Schiffermüller.
Axylia putris L.
Phalaena typica L.
Lampra fimbriata Schreber (*fimbria* L.).
Cerastis rubricosa Schiffermüller.
Anaplectoides prasina Schiffermüller (*herbida* Hübner).
Conistra vaccinii L.
Anchoscelis helvola L. (*rufina* L.).
Atethmia centrago Haworth (*aerampelina* Hübner nec Esper).
Citria lutea Ström (*flavago* Fabricius nec Schiffermüller, *silago* Hübner).
Cirrhia fulvago L. (*icteritia* Hufnagel, *cerago* Schiffermüller).
Agrochola circellaris Hufnagel.
A. lychnidis Schiffermüller (*pistacina* Fabricius).
Allophyes oxyacanthae L.
Cucullia chamomillae Schiffermüller.
C. umbratica L.
Calocampa exsoleta L.
C. vetusta L.
Graptolitha ornitophus Hufnagel (*rhizolitha* auctt.).
Xylocampa areola Esper (*lithorhiza* Borkhausen).
Griposia aprilina L.
Dryobota protea Schiffermüller.
Leucania conigera Schiffermüller.
L. comma L.
Orthosia incerta Hufnagel (*instabilis* Schiffermüller) (see p. 342).
O. gracilis Schiffermüller.
O. stabilis Schiffermüller.
O. cruda Schiffermüller (*pulverulenta* Esper, *ambigua* Hübner).
O. gothica L. (see p. 342).
Tholera popularis Fabricius.
T. cespitis Schiffermüller.
Hada nana Hufnagel (*dentina* Schiffermüller) (see p. 342).
Hadena cucubali Schiffermüller.
H. thalassina Hufnagel (see p. 342).
H. suasa Schiffermüller (*dissimilis* Knoch).
Diataraxia oleracea L. (*essonii* Hampson).
Melanchra persicariae L.
Anarta myrtilli L. (see p. 331).
Zanclognatha tarsipennalis Treitschke.
Z. nemoralis Fabricius (*grisealis* Hübner).
Hypena proboscidalis L. (fig. 44).
Euclidimera mi Clerck.
Ectypa glyphica L.
Rivula sericealis Scopoli.
Plusia chrysitis L.
P. festucae L.
P. iota L.
Abrostola tripartita Hufnagel (*urticae* Hübner).
A. triplasia L.
Orgyia antiqua L. (see p. 312).
Sterrha inornata Haworth (see p. 331).
S. biselata Hufnagel (*bisetata* auctt.).
S. dimidiata Hufnagel.
Scopula remutaria Hübner (*floslactata* Haworth).
Cosymbia pendularia Clerck (see p. 330).
Hemithea strigata Müller (*aestivaria* Hübner).
Jodis lactearia L.
Hipparchus papilionaria L.
Pseudoterpna pruinata Hufnagel (*cytisaria* Schiffermüller).
Mysticoptera sexualata Retz (*sexualisata* Hübner).
Lobophora halterata Hufnagel.
Chloroclystis rectangulata L.
Eupithecia albipunctata Haworth (*tripunctaria* Herrich-Schäffer).
E. vulgata Haworth.
E. pulchellata Stephens.
E. succenturiata L.
E. castigata Hübner.
E. plumbeolata Haworth.
E. pygmaea Hübner (*palustraria* Doubleday).
E. abbreviata Stephens.

- E. exigua* Hübner.
Eucymatoge subnotata Hübner.
E. scabiosata Borkhausen (*subumbata* Guenée).
Chesias legatella Schiffermüller (*spartiata* Fuessley).
Anaitis plagiata L. (see p. 342).
Lygris dotata L. (*pyraliata* Schiffermüller).
Epirrhoë alternata Müller (*sociata* Borkhausen).
Lyncometra ocellata L.
Chloroclysta miata L. (see p. 342).
C. siterata Hufnagel (*psittacata* Schiffermüller).
Hydriomena impluviata Schiffermüller (*coerulata* Fabricius, *trifasciata* Borkhausen).
Dysstroma truncata Hufnagel (*rusata* Schiffermüller).
Lampropteryx suffumata Schiffermüller.
Europheila badiata Schiffermüller.
Coenoteophria derivata Schiffermüller (*nigrofasciaria* Goeze).
Perizoma bifasciata Haworth (*unifasciata* Haworth).
P. alchemillata L.
P. flavofasciata Thunberg (*decorata* Hübner).
Pelurga comitata L.
Mesoleuca albicillata L.
Xanthorhoë spadicearia Schiffermüller (*ferrugata* auctt. nec Clerck).
X. designata Hufnagel (*propugnata* Schiffermüller) (see pp. 295, 342).
X. fluctuata L. (see p. 342).
Larentia cervinalis Scopoli (*cervinata* Schiffermüller, *clavaria* Haworth).
Ortholitha limitata Scopoli (*chenopodiata* auctt.).
O. mucronata Scopoli (*plumbaria* Fabricius, *palumbaria* Schiffermüller).
Calostigia multistrigaria Haworth.
C. didymata L.
C. pectinataria Knoch (*viridaria* Fabricius nec Clerck).
Orthonama vittata Borkhausen (*lignata* Hübner).
Alsophila aescularia Schiffermüller.
Ectropis punctulata Schiffermüller (*punctularia* Hübner) (see p. 331).
Cleora lichenaria Hufnagel.
C. rhomboidaria Schiffermüller (*gemmaria* Brahm).
Ematurga atomaria L. (see p. 331).
Erannis progemmaria Hübner (*marginaria* Borkhausen nec Villers).
E. defoliaria Clerck.
Phigalia pilosaria Schiffermüller (*pedaria* Fabricius).
Lycia hirtaria Clerck.
Biston betularia L.
Ligdia adustata Schiffermüller.
Lomaspilis marginata L.
Thera rupicaprararia Schiffermüller.
Bapta punctata Fabricius (*temerata* Schiffermüller).
Gnophos obscurata Schiffermüller (*obscuraria* Hübner, *pullata* Stainton) (see p. 331).
Lithia chlorosata Scopoli (*petraria* Hübner).
Dyscia fagaria Thunberg (*belgaria* Hübner) (see p. 331).
Cabera pusaria L.
Campaea margaritata L.
Plagodis dolabraria L.
Epione repandaria Hufnagel (*apiciaria* Schiffermüller).
Selenia lunaria Schiffermüller.
Colotois pennaria L.
Deuteronomos erosaria Schiffermüller.
Ennomos quercinaria Hufnagel (*angularia* Hübner).
Gonodontis bidentata Clerck.
Habrosyne pyritoides Hufnagel (*derasa* L.).
Thyatira batis L.
Hemaris tityus L. (*bombyliiformis* auctt., *scabiosae* Zeller).
Deilephila porcellus L.
D. elpenor L.
Smerinthus ocellatus L.
Laotroë populi L.
Pygaera pigra Hufnagel (*reclusa* Fabricius).
P. curtula L.
Notodonta ziczac L.
Pheosia tremula Clerck (*dictaea* Esper).
Gluphisia crenata Esper.

<i>Pterostoma palpina</i> L.	<i>Drepana lacertinaria</i> L. (lacertula Schifferrmüller).
<i>Cerura vinula</i> L.	<i>Poecilocampa populi</i> L.
<i>Phalera bucephala</i> L.	<i>Eriogaster lanestris</i> L.
<i>Saturnia pavonia</i> L. (carpini Schifferrmüller) (see p. 331).	<i>Macrothylacia rubi</i> L.
<i>Aphantopus hyperantus</i> L.	<i>Philudoria potatoria</i> L.
<i>Aglais urticae</i> L.	<i>Zygaena filipendulae</i> L.
<i>Cupido minimus</i> Fuessly.	<i>Procris statice</i> L.
<i>Callophrys rubi</i> L.	<i>Sphecia bembeciformis</i> Hübner
<i>Euchloë cardamines</i> L.	(crabroniformis Lewin nec Schifferrmüller).
<i>Cilia glaucata</i> Scopoli (spinula Schifferrmüller).	<i>Hepialus hectus</i> L.

To which may be added the typical subspecies of *Calaena leucostigma*, *Leucania pallens*, *Eupithecia venosata*, *E. absinthiata*, *E. satyrata*, *E. tenuiata*, *Operophtera brumata*, *Oporinia dilutata*, *O. autumnata*, *Cleora repandata* and *Eumenis semele*, the marsh races of *Lygris testata* and *Hydriomena furcata* and the woodland race of *Diarsia festiva*.

The occurrence in Ireland of almost 60 per cent. of the species and races listed in this chapter is sufficient evidence for the existence of a postglacial land-connection between Great Britain and Ireland. The ranges of the species demonstrate its former position.

It will be noted that only a very small number of the non-Irish species have ranges in Great Britain which extend as far north as the Clyde, the great majority being confined to the southern half of England. On the other hand, the great majority of the Irish species have ranges in Great Britain which extend at least as far north as the Clyde, only a small number not occurring north of the Southern Uplands. This indicates that in order for a species to have spread into Ireland in postglacial times it was first necessary for it to have spread at least as far north as the Clyde in Great Britain. Thus the postglacial land-connection between the two countries must have extended from a point in western Scotland not far north of the Clyde to northern Ireland.

There is other evidence to indicate that this was its probable position. At present Great Britain and Ireland are separated by depths of sea greater than 30 fathoms except at one point: a submarine ridge less than 30 fathoms below the surface connects Islay, on the west of Scotland with Inishowen, in the north of Ireland (fig. 45). This ridge coincides perfectly with the site of the land-connection as indicated by the Lepidoptera. It is generally agreed that the sea was at least 30 fathoms below its present level in the region of the Dogger Land during the early part of the postglacial and thus it must have been relatively low in this region also. However, there is a possibility that it may not have been 30 fathoms lower than its present level in relation to western Scotland and northern Ireland at that time, as the land there may not have fully recovered from the isostatic sinking it underwent during the third glacial phase. This could have been counteracted by the ridge having been higher than now in the early postglacial, its height since having been reduced by erosion both before and after its submergence.

In Great Britain the majority of the postglacial arrivals are concentrated in the south and east—at what was the termination of the British–Continental land-connection. But in Ireland the majority are not concentrated near what was the termination of the Islay–Inishowen land-bridge. The reason for this apparent anomaly is that in Great Britain climatic and other ecological conditions become progressively less favourable to the species the farther one goes from the termination of the former British–Continental land-connection, while in Ireland conditions are not any more unfavourable—in fact they are more favourable—in the south than in the north: in both countries the annual temperatures, for example, are lower in the north than in the south.

Some of the species listed above have northerly distributions in Ireland. These distributions are unlikely to be due primarily to present-day climatic conditions as the distributions of such species in Ireland contradict their distributions in England: in one country the species have their headquarters in the cooler regions, in the other in the warmer. The obvious explanation for their northerly distributions in Ireland is that they invaded the country from the north and have not spread sufficiently to colonise the whole country, either because they have not had time to do so or because they did not arrive in sufficient numbers and concentrations before the severance of the Islay–Inishowen land-bridge.

The reasons why some species have southerly distributions in Ireland also can be explained. Eighteen such species are listed above and it will be noted that the ranges of only two of them extend north of the Clyde, eleven of the species being confined to the southern half of England. In other words, the majority of these species have ranges which reach neither the Irish nor the Scottish termination of the Islay–Inishowen land-connection. However, during the Atlantic period, when the climate of the British Isles was warmer than now, they may have spread into southern Scotland and thence into and throughout Ireland, later to become extinct towards the northern limits of their original ranges in both countries as a result of the climatic deterioration of the later postglacial.

It is quite possible, however, that in some instances the southerly distributions in Ireland may be due to the species having been Pleistocene arrivals which have had a similar history to, for example, *Leptidea sinapis* or the species listed on pp.333-4, but in the absence of taxonomic evidence it is impossible to suggest their identities.

There remain the few species whose ranges in Great Britain do not extend north of the Southern Uplands but whose Irish ranges cover the whole of that country. Most of these may have had their British, but not their Irish, ranges reduced by the climatic deterioration of the later postglacial, but there is a possibility that some may have been Pleistocene arrivals. This may have been the case with *Eilema complana*, which inhabits heaths, and thus probably could have survived a glacial phase, and which exhibits some local racial variation in England. *Celastrina argiolus* and *Argynnis paphia* are further possible examples.

The first may have had a history similar to *Ascia cinctaria* (p. 346), which, like *argiolella*, feeds on holly. The second species exhibits some local variation, Irish females being larger than British, and there is some indication that a local race occurs in Devon (Pagley, 1923). These examples lend emphasis to the point that there is a strong possibility that a considerable proportion of the species listed in this chapter were originally Pleistocene arrivals in the British Isles.

The ranges and distributions of most of the suspected migrants (pp. 279-286), for which there is no evidence of a Pleistocene origin are such as to indicate that they arrived in the British Isles mainly by spreading over the early postglacial land-connections and that establishments by overseas migrations have, in most cases, been relatively negligible in importance. Like the non-migratory postglacial arrivals discussed above, most of the suspected migrants whose ranges in Great Britain do not reach the Clyde either do not occur in Ireland (*Nemargia flandria*, *Acanthia pascuicola*, *Cirrus gilvago*, *Cuscuta aenea*, *Emmelia trabealis*, *Sierria marginata*, *Scopula rubiginata* and *Gastropacha quercifolia*), or have southerly distributions there (*Lithonia quadra*, *Scopula imitaria* and *Melicossoma novaeana*), while all the species whose ranges extend at least as far north as the Clyde occur in Ireland and have wide ranges there. Most of them have ranges which cover the whole of Ireland, but some—again like some of the non-migratory postglacial arrivals—have northerly distributions there (*Lycia hirtaria* and *Chimarra clathrata*).

By the end of the Atlantic period the great majority of the existing Lepidopterous inhabitants of the British Isles had become established. The only species yet to arrive were those which were deliberately or accidentally introduced by man (see pp. 273-4) and the species, probably very few in number, which became established by overseas migration.

X. CONCLUSIONS.

a. The Development of the British Lepidopterous fauna.

The chief conclusions arrived at in the foregoing chapters may be summarised briefly.

The existing species of Macrolepidoptera all became established originally in the British Isles by migration from abroad. The great majority arrived by spreading over land-connections which no longer exist, most of them from what is now the European mainland, but at least one arrived from the region of Ireland.

There is no evidence which could be interpreted as indicating that any species dates wholly from before the Upper Pleistocene Glaciation as an inhabitant of the British Isles. The only possible survivors from the Third Interglacial Period for which evidence exists are a few "Lusitanian" forms found in south-west Ireland.

The main invasions took place during two periods: during the first interstadial phase of the Upper Pleistocene Glaciation and in

postglacial (Holocene) times. A relatively minor invasion of species characteristic of temperate or cool temperate climates took place during the second interstadial phase. Species characteristic of cold climates arrived during three periods: during the three glacial phases of the Upper Pleistocene. These invasions were less important as to the number of species involved than the first interstadial and the postglacial invasions.

The glacial phase arrivals survived the more temperate periods mainly on the mountains of the north and west, where most of them have their headquarters at the present day. The interstadial phase arrivals survived the glacial phases mainly on the ice-free regions in the south and on the now-submerged glacial land which existed around the present coasts of the British Isles. In order to survive some were forced to change their food-plants or habitats. Of these, some became adapted for life on the sea-coasts, some for life on heaths and moorlands and some for life in fens and marshes. The interstadial survivors now have their headquarters mainly in the southern, south-western and western parts of the British Isles. The postglacial arrivals have their headquarters in the south and east of Great Britain and most of them have ranges which cover the whole of Ireland.

In comparatively recent times relatively small numbers of species became established in the British Isles by overseas migration from abroad or by artificial introductions due to human agency.

The proportions of the total number of the species of *Macrolepidoptera* now resident in the British Isles, which it is suggested probably arrived during each period, are indicated in the following table:—

<i>Date of Arrival.</i>	<i>Per cent. dating wholly from each period.</i>	<i>Per cent. dating partially from each period and partially from other periods.</i>
Third Interglacial Period ...	0	+ 1
Upper Pleistocene Glaciation	+34	+13
(a) 1st glacial phase ...	+ 3	+ 3
(b) 1st interstadial phase ...	+10	+ 6
(c) 2nd glacial phase ...	+ 5	+ 1
(d) 2nd interstadial phase ...	-10	+ 2
(e) 3rd glacial phase ...	- 6	+ 1
Postglacial (Holocene) ...	-48	-23
(a) Pre-Atlantic arrivals ...	-46	+15
(b) Artificial introductions ...	- 1	-- 1
(c) Overseas migrants ...	- 1	+ 7

Thus it would appear that at the very minimum 47 per cent. of the species have been established in the British Isles since before the end of the Ice Age and a minimum of 34 per cent. date wholly from Pleistocene times.

Because of the absence of palaeontological evidence the foregoing reconstructions of the species' histories are of necessity almost entirely theoretical, and therefore controversial. The evidence on which the reconstructions are based often is so vague and uncertain that the reconstructions of the histories of many species is largely a matter of opinion.

There are various ways in which ecological, taxonomic and zoogeographical evidence may be misleading. One is that in utilising such evidence one is forced to make certain reasonable assumptions which almost certainly apply to the great majority of the species but which may not hold good with some. For example, in the absence of any evidence to the contrary it is assumed that most species have not changed their food-plants or other ecological requirements within the past 100,000 years, and that past distributional changes have been caused primarily by past ecological changes. Possibly there are species whose habits, and consequently distributions, have changed radically within comparatively recent times, but except when this has occurred within the past century no evidence of their identities normally exists. A second difficulty is that the true distributions of some species may not be fully known. If at some future date species are discovered in localities outside their present known ranges, or if some of their existing records are found to be incorrect, then it may be necessary to revise the theories as to their histories which are based primarily on zoogeographical evidence. Similar revisions may be necessitated by future taxonomic and more importantly, ecological studies. Finally, future geological investigations may render it necessary to revise the histories of certain species in order to bring them in line with the new information.

All this lends emphasis to the point that the study of the origin and history of the British Lepidopterous fauna is still in its infancy. However, the objections mentioned above are applicable to reconstructions of the histories of any non-fossil group of animals and are of less importance with the Lepidoptera as relatively more is known of the habitats, variation and distributions of these insects than of other groups of animals.

(b) Past Geographical, Climatic and Vegetational Changes indicated by the Lepidoptera.

Past geographical and climatic changes indicated by the Lepidoptera, apart from those indicated by geological evidence, have been discussed previously but may be summarised here. Geographical Changes : (a) The British Isles formed part of the European land-mass during most of the Upper Pleistocene ; (b) they were connected to the Faroes and to Iceland by land during the first glacial phase of the Upper Pleistocene and during part of the first interstadial phase ; (c) St. Kilda probably has been isolated by the sea from the Scottish mainland since the second glacial phase, and the Shetlands, Outer Hebrides and certain of the Inner Hebrides (Canna, Rhum, Eigg, Muck, Coll, Tiree) since the end of the second interstadial phase ; (d) the only

postglacial land-connection between Great Britain and Ireland extended between Islay, on the west of Scotland, and Inishowen, in the north of Ireland. The more important characters of the climate were : (a) The first interstadial phase was dry and sunny and was at least partially warmer than now ; (b) during the second and third glacial phases there were areas in the southern part of the North Sea and of the Irish Sea where the climate was more temperate than that of the regions to the north, west and east of these areas ; (c) during the glacial phases the climate of the south-western parts and of the western coasts of the British land-mass was relatively mild, the winters probably being no colder than now ; (d) during the second interstadial and third glacial phases the climate of Ireland was more oceanic in relation to that of Great Britain than at present. The summers in Ireland probably were wetter during the third glacial phase and the winters perhaps warmer during both these phases than they are at present.

Analyses of the food-plants of the Pleistocene survivors indicate to some extent the composition of the vegetation of the ice-free parts of the British land-mass during the glacial phases, as if a species of *Lepidoptera* survived a glacial phase in a particular area then its food-plant must have survived there also.

To take first the first interstadial phase arrivals. There are some of these which must have survived the second glacial phase on the now-submerged glacial land west of Scotland. The habits of *Brachionycha nubeculosa* indicate that birch was the only deciduous tree to survive the second glacial phase there, and that it did survive is further indicated by such birch-feeding species as *Semiothisa notata*, *Tethea fluctuosa*, *Endromis versicolora* and *Aegeria scoliaeformis*, to mention only the better examples. It is possible that pine survived there, the evidence being provided by *Itama brunneata* as well as by the variation of the tree itself. *Eupithecia intricata*, *E. sobrinata*, *Thera cognata* and *T. juniperata* provide strong evidence for the survival of juniper, and *Isturgia limbaria* indicates the existence there of broom. The habits of *Cleora cinctaria* and *Selidosema plumaria*, of the presumed first interstadial races of such species as *Celaena leucostigma*, *Diarsia festiva*, *Eupithecia absinthiata*, *E. satyrata*, *Lygris testata*, *Hydriomena furcata*, *Operophtera brumata*, *Oporinia autumnata*, *Ectropis bistortata*, *Lasiocampa quercus* and *Trichiura crataegi* and of the Inverness race of *Carterocephalus palaemon* indicate that all the following plants, most of which must have spread over the British Isles during the first interstadial, were exterminated there, at least inland : alder, *Salix*, hawthorn, blackthorn, *Hypericum*, *Artemisia*, *Lotus*, *Vicia*, *Rumex*, *Genista*, *Senecio*, *Dorycnium*, *Achillea*, *Cladium*, *Iris*, *Brachypodium* and *Bromus*. They were replaced by a flora which included bilberry, heather, heath and *Molinia* and other grasses. However, in dry and well-drained situations some of these plants did survive—plants such as *Lotus*, *Cerastium*, *Achillea* and *Trifolium*. This is indicated by the survival of such species as *Nyssia zonaria*, *Zygaena purpuralis* and *Z. achilleae*. West of Scotland the latter plants probably survived mainly on the coastal sandhills, where the soil was sufficiently well drained and where they were affected

by the relatively mild climates of the coasts. On the land west of Ireland, where the vegetation appears to have been similar to that on the land west of Scotland, these plants survived in similar situations and probably also in the well-drained limestone districts.

It is probable that birch was more common on the extensive area of land which existed south and south-west of the British Isles during the second glacial phase, as on that land a larger number of birch-feeding species survived. *Epione paralellaria* and *Leucodonta bicoloria* are examples additional to those mentioned above. *Thera variata* and *Eupithecia pusillata* provide evidence that spruce—a tree known to have been present in Great Britain in first interstadial times—survived on the land south-west of England. *Eupithecia denotata* provides evidence that *Campanula trachelium* died out but that *Jasione montana* survived.

Generally speaking the evidence indicates that heath and moorland vegetation covered most of the now-submerged land which existed west and south of the British Isles during the second glacial phase, birch being the dominant tree and being relatively common in the south. It is probable that the common maritime plants, such as *Lychnis*, *Silene* and *Statice*, survived all along this coast-line: this is indicated by the maritime Lepidoptera discussed in Chapter VI (a). The survivals of such species as *Setina irrorella* and *Cryphia muralis* indicate that, in some regions at least, conditions were favourable for the growth of lichens.

In the Midlands of England—the region just south of the ice-fronts—heath and moorland vegetation must have been dominant. The habits of *Epicnaptera ilicifolia* indicate that *Salix* (and ? birch) died out there but that bilberry survived. *Aegeria scoliaeformis* and *Leucodonta bicoloria*, however, indicate that birch did exist there. The same plants which survived on the western glacial land appear to have survived in southern England. There is some evidence that relatively warmer regions existed in the areas now occupied by the Irish Sea and North Sea. Birch, juniper and *Helianthemum* were amongst the plants which existed in the former region, and it seems not unlikely that the vegetation of this low-lying area was very similar to that of the south-western parts of the glacial land. During the second glacial phase the Dogger Land region apparently became covered by dense forests, probably of pine (see p. 306). This may have taken place during the latter part of the phase. On the sea-coasts and in the fens and marshes the vegetation probably was similar to that of these situations at the present day. All or most of the plants which survived elsewhere in the British land-mass probably existed in that region, but there were also some others. Thus, *Malacosoma castrensis* and *Euchloris smaragdaria* indicate the survival of *Artemisia* and other salt-marsh plants, *Apatele strigosa* that of hawthorn, *Lymantria dispar* that of some deciduous trees, perhaps birch, *Papilio machaon* that of *Peucedanum palustre*, *Lycaena dispar* that of *Rumex hydrolapathum*, and several other species that of grasses. On the other hand, various *Umbelliferae* and other small plants such as *Achillea* and *Poterium*, which must have

existed in that region in second interstadial times, became extinct there during the second glacial phase; this is indicated by the species which have changed their food-plants (see pp. 305-6).

Additional plants which were present on the ice-free areas of the British land-mass during the second glacial phase include bearberry, crowberry and *Myrica*. Their presence is indicated by the second glacial phase arrivals.

All the plants which survived the second glacial phase also must have survived the third, and there were some additional survivors. That oak probably existed in southern England and on the glacial land south-west of the British Isles during the third glacial phase is indicated by *Drymonia ruficornis*, *D. dodonea* and *Thecla quercus*, which feed only on this tree, supported by *Herminia barbalis* and *Boarmia punctinalis*, which feed on oak and birch, and by *Eilema sororcula* and *Cleora glabraria*, which feed on lichens on oak. That birch was common in those regions is indicated by such species as *Cosymbia pendularia*, *Ectropis consonaria*, *Amathes ditrapezium* and *Odontotia carmelita*, in addition to the first interstadial survivors mentioned above. The existence there of wych elm is shown by *Abraxas sylvata* and *Discoloxia blomeri*, of *Salix* by *Earias clorana* supported by *Cepphis advenaria* and *Anagoga pulveraria*, of huckthorn by *Gonepteryx rhamni* and *Philereme vetulata*, and of blackthorn by *Bapta bimaculata* and *Thecla betulae*. *Craniophora ligustri* and *Eupithecia innotata* ssp. *fraxinata* may indicate the survival of ash, *Acasis viretata* that of holly and *Orthosia populi*, *Zenobia subtusa* and *Sesia apiformis* that of *Populus* (probably aspen). The smaller plants included various grasses and herbs, such as *Stachys*, *Galium* and *Valeriana* in addition to those mentioned above.

The indications are that during the third glacial phase most of England and of the southern and south-western parts of the Irish land-mass was covered with an open woodland in which birch was dominant and oak probably common. There seems to have been an abundance of smaller plants, chiefly plants characteristic of heathy or marshy situations.

On the land west and east of the Highland ice-sheet the vegetation seems to have been similar in composition to that of the western glacial land during the second glacial phase, except that birch probably was relatively more abundant.

(c) *The Rate of Evolutionary Change in Lepidoptera.*

The endemic racial variation exhibited by populations of Lepidoptera which probably have been isolated in the region of the British Isles for known lengths of time provides some indication of the rate at which evolutionary change may take place amongst these insects.

As there are probably no endemic British species it is apparent that in no case has a population been isolated in this region for a sufficiently long period for specific characters to have developed. As some species probably date from the first glacial phase of the Upper Pleistocene it may be concluded that the time which has elapsed since then—

some 120,000 years—was not sufficiently long for the development of specific characters. Zeuner (1946) concluded that at least 500,000 years normally is necessary for the development of new species; no evidence to the contrary is provided by the British Lepidoptera.

Many of the first interstadial species have developed strong subspecific characters in the British Isles. In some cases the endemic British subspecies differ so markedly from those found elsewhere as to be regarded by some writers as being distinct species. Good examples are *Eilema pallifrons* ssp. *pygmaeola*, *Amathes ashworthii* ssp. *ashworthii*, *Hadena andalusica* ssp. *barrettii*, *Sterrha dilutaria* ssp. *holosericata*, *Eupithecia denotata* ssp. *jasioneata* and *Oporinia autumnata* ssp. *filigrammaria*. These subspecies developed in large populations and must have developed their subspecific characters since the end of the first interstadial phase—in less than 90,000 and probably in about 50,000 years. The heath races listed on pp. 309-314 developed in about the same length of time, as did the Dogger Land races discussed on pp. 304-6.

Only some populations which have been isolated in the region of the British Isles since the first interstadial phase have developed subspecific characters. Many have not developed any racial variation in the same length of time.

Smaller populations may develop racial variation in a much shorter time. For example, the ssp. *anglicata* of *Eupithecia intricata* and the ssp. *thulei* of *Diarsia festiva* probably have developed since the third glacial phase—in about 25,000 years. The former developed in a population which was isolated in the east of Scotland by the advance of the Highland ice-sheets, the latter in a population which was isolated in the Shetlands by the rising sea. Further examples are the ssp. *cassiteridum* and ssp. *splendida* of *Maniola jurtina* and the Hebridean race of *Euphydryas aurinia* ssp. *praeclara*. These developed, from *iernes* and from typical *praeclara* respectively, when the populations of the species which had survived since the first interstadial had their ranges divided by the rising sea during the third glacial phase. This division of their ranges permitted the inhabitants of the western parts and islands of Great Britain to develop independently of the inhabitants of Ireland.

Relatively very small populations may, in some cases, have developed racial variation within postglacial times. The only definite example appears to be *Lycaena dispar*. During the isolation of a population on the Dogger Land it developed subspecific characters distinguishing it from the ssp. *rutilus*. This probably took tens of thousands of years to take place—since at least the second interstadial phase and probably since the first. This population was exterminated by the postglacial submergence of the Dogger Land some 8,000 years ago, except for two small colonies, one in England and one in Holland. Since that time the two colonies have developed independently of each other, one becoming the ssp. *dispar*, the other the ssp. *batauius*. There is some possibility that such species as *Pachetra sagittigera* and *Zygaena meliloti*, which have very restricted ranges in southern England, may have been postglacial arrivals which developed their subspecific characters in about the same length of time.

It is necessary to mention that the estimates given above might be rather low, as some species may have developed variation in the form of a cline before the isolation of the populations which are now regarded as being distinct subspecies. For instance *L. dispar* may have exhibited variation in the form of a cline grading from *dispar* in the west of the Dogger Land region to *bataivius* in the east. The intermediate stages in the cline may have been exterminated by the submergence of the Dogger Land and the surviving colonies may not have developed independently to any appreciable extent since. The same may apply to *M. jurtina* and *E. aurinia*.

In Pleistocene times the lepidopterous inhabitants of the region of the British Isles were subjected to great environmental changes from which there was no escape. During each interstadial phase the survivors from the previous glacial phases must have inhabited the mountains of the north and west, and in order to survive there were forced to endure any climatic changes which took place. Similarly, during the glacial phases the interstadial survivors were isolated in a relatively temperate region bounded in the west and south-west by the sea and in the north east and south-east by the British, Scandinavian, Alpine and Pyrenean ice-sheets and by zones where tundra conditions existed and relatively continental climates prevailed. Because of this, subspecific characters may have developed more rapidly in the region of the British Isles than elsewhere. In larger land-areas the species could move from one region to another in accordance with changing environmental conditions and there the rate of evolutionary change may have been much less rapid. Probably the estimate of 50,000 years as a fast rate for subspecies-development in large populations is exceptionally low and applicable only to populations which were forced to endure extreme environmental changes.

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The information on which the reconstructions of the histories were based was compiled from various textbooks on the British Lepidoptera, notably those of Barrett (1892-1907), Ford (1945), Frohawk (1924, 1934), Meyrick (1928), Newman and Leeds (1913), Scorer (1913), South (1939, 1941) and Tutt (1891, 1899-1909, 1901-5), and from various entomological and natural history periodicals and local lists. The chief works consulted are listed below in addition to the references mentioned in the text.

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A REVISION OF THE GENUS *DYSDERCUS* BOISDUVAL (HEMIPTERA, PYRRHOCORIDAE), EXCLUDING THE AMERICAN SPECIES

BY PAUL FREEMAN, M.Sc., A.R.C.S., F.R.E.S.

E. H. N.

Manuscript received 10th November, 1946.

(Read 4th June, 1947)

WITH FIFTY-NINE TEXT-FIGURES.

INTRODUCTION AND ACKNOWLEDGEMENTS.

THIS revision was undertaken primarily on account of the importance of species of *Dysdercus* Boisduval as vectors of the spores of fungi causing "staining" of cotton. The original intention was to revise the whole genus but, owing to the limited amount of time available, it has been found necessary to curtail the work and to confine it to an account of the species from the Ethiopian, Oriental and Australasian Regions only. Throughout, reference has been made only to these species, an important point in the diagnosis of the genus.

The material used was that in the collection of the British Museum supplemented by a small collection from the National Museum of Prague, lent through the kindness of Dr. Ludvik Hoberlandt, and by some specimens of three species preserved in alcohol sent to me from S. Rhodesia through Mr. B. L. Mitchell. The work was carried out in the British Museum and in the Department of Entomology of the Imperial College of Science and Technology, London, under the general direction of Professor J. W. Munro. I wish to express my thanks to Mr. W. E. China of the British Museum who gave me much advice on some of the more difficult problems, and to Mr. E. O. Pearson of the Empire Cotton Growing Corporation for his assistance with the Ethiopian species. Mr. Pearson was also kind enough to place at my disposal a manuscript key, drawings and notes prepared by him for the American species, based on material in the American Museums, a manuscript which I have unfortunately been unable to use.

HISTORICAL SURVEY AND DISCUSSION.

This is the first time that an attempt has been made to give a comprehensive taxonomic revision of the species of *Dysdercus* from the Ethiopian, Oriental and Australasian Regions. Earlier work has included some account of the African species by Stål in his *Hemiptera Africana* (1865) and, mainly a catalogue of the world species, in his *Enumeratio Hemipterorum* (1870a), a key to the African species by Schouteden (1912) and notes by Bergroth (1914) on the synonymy of the species long confused with *D. cingulatus* (Fabricius). Hussey's *Catalogue of the Pyrrhocoridae*, 1929, is invaluable, but nowhere are actual descriptions brought together and compared.

In general the African species are well known, and Schouteden's key includes practically the same species that I have included in this

paper. However, the characters used by him are not all particularly satisfactory and he has made no attempt at a natural classification or grouping. The Oriental and Australasian species have been much confused in the past and a number of species founded on insecure bases: this is only to be expected when descriptions are so vague, scattered and seldom draw attention to the differences between species.

A study of the long series of some of the species in the collection of the British Museum showed that some of the characters, such as colour or shape of prothorax, used by previous authors are extremely variable. It was therefore necessary to try to find good structural characters to group and separate the species and then by building on this basis define those other characters, colour or structural, which could be used with confidence. The first attempt at this was made by Breddin (1909) when he separated some of the species confused with *D. cingulatus* (Fabricius), but he used only the external configuration of the ninth segment of the male. This same character has since been used by Blöte (1931), but it is a difficult character to describe and appreciate and does not group the species beyond separating four African species.

Good characters for grouping and separating most of the species lie in the parameres, vertical processes of the ninth segment (see below) and aedeagus of the male, supplemented by the general shape of the ninth segment of the male and details of the spermatheca of the female. I have used only these characters for grouping the species, and mainly, but not entirely, these same characters, usually excluding the spermatheca, for species separation. Practically every species is also definable on colour and other characters, which I have described in full, but, as peculiar colour forms are continually being found, examination of the male genitalia is, in most species, advisable whenever there is doubt.

In the descriptions of species I have first put structural and genital characters, followed these by the colour of dorsal and ventral surfaces, and finally drawn attention to the important features in a brief summary. I have not used a colour code in the descriptions as that seems hardly necessary and is rather cumbersome: a plain statement of colour in terms of red, yellow, orange, etc., is perfectly satisfactory, particularly in view of the variability.

Many of the African specimens in the British Museum were collected by S. A. Neave; I have followed details of these specimens by the initials S. A. N.

In the main, reference has been made to systematic papers only, but papers referring in detail to biology or breeding experiments have been mentioned under the species concerned. Papers describing a number of species are Hargreaves and Taylor (1937) for the Uganda species and Mumford (1926) for a general account of the World species.

Dysdercus Boisduval.

Dysdercus (Serville MS) Boisduval (1835) in part, Amyot and Serville (1843), Herrich-Schäffer (1835) in part, Stål (1855), Signoret (1858) in part, Montrouzier (1861), Signoret (1861), Stål (1861), Stål (1866), Mayr (1868), Stål (1868), Stål (1870a and b), Walker (1872) in part, Gerstaecker (1873), Butler (1879), Distant (1879), Lethierry (1883a and b), Distant (1884), Reuter (1887), Distant (1888), Carpenter (1891), Kirby (1891), Gerstaecker (1892), Karsch (1892), Bergroth (1894), Karsch (1894), Bergroth (1895),

Haglund (1895), Breddin (1900), Kirkaldy (1900), Breddin (1901a, b, c, d and e), Kirkaldy (1901), Distant (1902a and b), Distant (1904), Breddin (1905a and b), Kirkaldy (1905), Schouteden (1905), Kirkaldy (1908), Banks (1909), Breddin (1909), Distant (1909a and b), Distant (1910), Schouteden (1910), Schouteden (1912 in part, Schumacher (1912), Bergroth (1913), Distant (1913), Matsumura (1913), Bergroth (1914), Distant (1914a and b), Horváth (1914), Heymons (1915), Horváth (1919), Bergroth (1920) in part, Distant (1920), Couteaux (1922), China (1924), Bergroth (1926), Esaki (1926), Tauber (1927), Hassey (1929) in part, China (1930), Blöte (1931), Schmidt (1932), *Cimex* Fabricius (1775, 1781 and 1787) in part, Goeze (1778) in part, Thunberg (1784) in part, Gmelin (1788) in part, *Lygaeus* Fabricius (1794, 1798 and 1803) in part, Wolff (1802) in part, Spinola (1837) in part, Montrouzier (1855) in part, *Astemma* Laporte (1833), Blanchard (1840), Kirkaldy and Edwards (1902) in part, *Pyrrhocoris* Hahn (1834) in part, Burmeister (1835) in part, Herrich-Schäffer (1844), Schaum (1862), *Dindymus* Walker (1873) in part, *Disdercus* Del Guercio (1918).

Date of genus *Dysdercus* Boisduval and genotype fixation.

The genus *Dysdercus* was first fully described by Amyot and Serville (1843), who included one species, *D. koenigii* (Fabricius). Previous authors have always regarded Amyot and Serville (1843) as founders of the genus and this single included species automatically as the genotype. However, Boisduval in 1835 described three species, *decussatus*, *oceanicus* and *pyrochroa*, which he placed in the genus *Dysdercus* (Serville MS). The inclusion of these three species (*pyrochroa* is not now included in *Dysdercus*) is sufficient indication of the genus, which thus, in my opinion, dates from 1835 and not 1843 and has as its valid author Boisduval and not Amyot and Serville. This means that *D. koenigii* (Fabricius) cannot be the genotype as it is not one of the originally included species. As no previous author seems to have fixed the genotype, I therefore designate *Dysdercus decussatus* Boisduval, 1835 as genotype of the genus *Dysdercus* (Serville MS) Boisduval, 1835.

Characters of *Dysdercus* Boisduval.

Distinguished from other genera of PYRRHOCORIDAE by acute apical angle to hemelytra and absence of hamus in cell of hind wing.

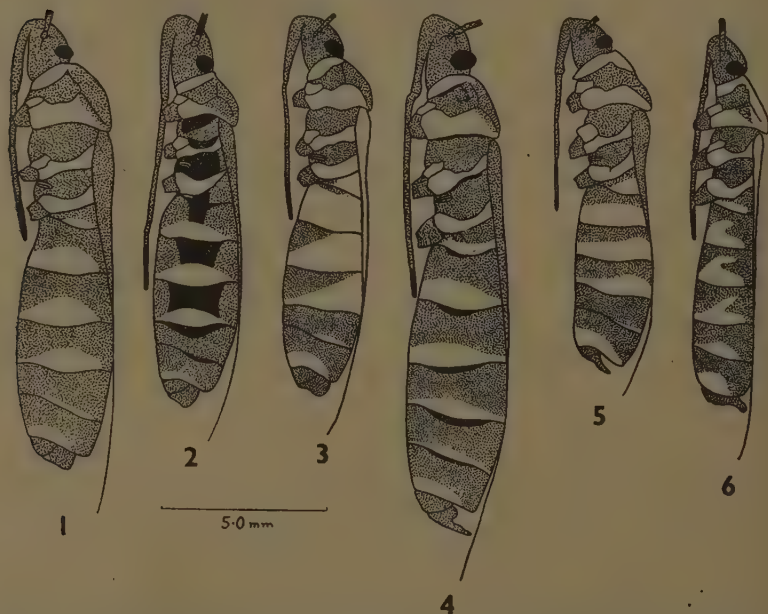
Form: Medium sized, elongate species, apical angle of hemelytron somewhat acute, giving a characteristic and easily recognisable appearance. *Sculpture*: Whole surface including prothoracic fold covered by minute sculpture, giving rather a matt appearance particularly on the dorsal surface. Collar and disc of prothorax punctured fairly closely and strongly, punctures around the margins often tending to be arranged in short folds, punctures of *D. oceanicus* Boisduval exceptionally sparse: scutellum normally impunctate, but with strong basal punctures in species allied to *D. decussatus* Boisduval: hemelytra with punctures rather closer and stronger than prothorax: ventral surface of thorax usually bearing punctures on the white coloured portions only, sometimes practically absent (*D. oceanicus*), sometimes almost rugose (*D. evanescens* Distant): ventral surface of abdomen impunctate except for sixth segment apically and genitalia: abdomen with triangular area in middle of each segment laterally slightly rugose. *Head* medium sized, triangular, eyes moderate (figs. 7-10): longer in *D. longiceps* Breddin and *D. fasciatus* Signoret. Antennae with first and fourth segments subequal, second one and a half times as long as third: first segment usually slightly longer than second, but not always so, and can to a limited extent be used as a specific character: first segment reddish or yellowish basally, remainder of antenna black or dark except in *D. argillicus* Bergroth, which has fourth segment ochraceous, and nymphs of *D. cardinalis* in which fourth segment white basally.

Rostrum reaching well onto abdomen, in *D. mesiostigma* Distant to sixth segment, but usually to second or third; exact length variable but can be used as a specific character; first and second segments and third and fourth usually subequal, except in those with long rostra, when third segment often elongate; fourth and sometimes third segment dark, remainder pale. *Thorax*: Lateral margins of prothorax straight or sinuate, somewhat explanate (figs. 7—10), but very variable within each species. Anteriorly, prothorax thrown into a fold which is marked off posteriorly by a straight or nearly straight transverse furrow and anteriorly by a crescentic one which marks off a distinct anterior collar. Anterior angles variable but usually touching or nearly touching eyes; posterior angles rounded, often with a shallow fovea. Metathoracic scent gland spout usually clearly visible but may be indistinct.

Legs: Anterior femora bearing a small group of spines sub-apically, some anteriorly and some posteriorly, the tibia closing between; anterior femora also often spined ventrally along the whole length and then rather thicker than other femora. Middle and posterior femora always unarmed.

Male genitalia.

A full description is given in the next section.



FIGS. 1-6.—Lateral view of males; red areas shaded. (1) *D. superstitiosus* (Fabricius); (2) *D. fasciatus* Signoret; (3) *D. cardinalis* Gerstaecker; (4) *D. intermedius* Distant; (5) *D. haemorrhoidalis* Signoret; (6) *D. olivaceus* (Fabricius).

Female genitalia.

The cuticular lining of the spermatheca, its duct and accessory gland, afford characters useful in the grouping of species (figs. 15-20).

Spermatheca spherical or ovoid; duct coiled, long or short; accessory gland, opening at same point as spermatheca but absent in some African species, a simple tube, in most species recurved. Length of both duct and accessory gland varies within limits within each species but main features are constant.

Coloration.

Nearly all species are coloured according to a common pattern.

Dorsal surface: Head red or rarely black; prothoracic collar white or, rarely, concolorous with fold; prothoracic fold and lateral margins concolorous, red, orange, yellow or rarely black, fold often infuscated but dark colour does not spread to lateral margins; disc of pronotum, clavus and corium concolorous, usually some shade of yellow, orange or grey; prothorax often with a black band posteriorly but actual margin always narrowly pale; scutellum black, yellow or red; coria usually bear a fascia, either as two black spots or as two black lines, one on each wing, with a formation characteristic of the species; often an indication of paleness on coria along claval and membranal sutures, culminating in a definite pale X-cross in *D. decussatus*; membrane dark or black, rarely pale, always with a pale apical margin.

Ventral surface: Thorax with episterna red or infuscated, epimera and coxal cavities and prothoracic collar white; abdominal sternites each with a white band posteriorly, anteriorly red or infuscated, producing a fasciated pattern varying from species to species (figs. 1-6), but white fascia on segment 5 always narrow or missing and on segment 6 in the form of a crescent, seen in ventral view; occasionally a tendency for white to spread both sides of lateral triangular rugose area (fig. 6).

Male genitalia of *Dysdercus* Boisduval.

The ninth segment, as in other Heteroptera, is ring-like, surrounding a genital chamber which contains the aedeagus and associated parts (figs. 11 and 12). The external appearance of the ninth segment varies from species group to species group and can sometimes be used as a specific character (figs. 21-26). In the Oriental species the apical margin is ventrally slightly prolonged, and upturned, the extent and shape of the upturning being of some use as a specific character; in some African species the ventral apical margin is greatly prolonged into a conical process (fig. 24). Dorsally, above the genital chamber, lies the tenth segment bearing the anus. The aedeagus lies within the genital chamber with the parameres on either side in special cavities.

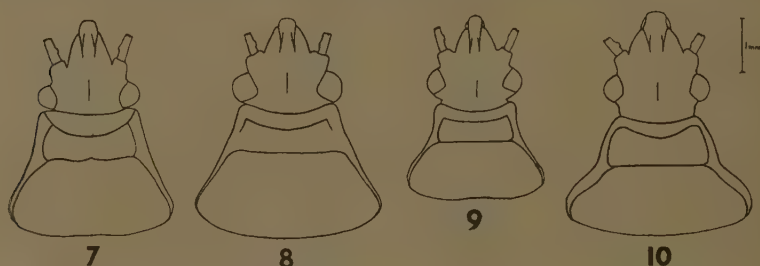
The aedeagus, arising, as is normal, from a basal plate (figs. 12 and 13), is usually retracted but with care may be expanded as in fig. 13. It can then be seen that there are three pairs (not two as stated by Singh-Pruthi) of conjunctiva appendages and that most of the aedeagus is membranous. The presence of a thorn-like branch to the second conjunctiva appendage (fig. 14) is used in the definition of the *D. decussatus* species group. The basal plate is attached by membrane to the general body wall and there is also a special lateral attachment (not shown) of the aedeagus base associated with the parameres. There is, however, an additional structure which secures the aedeagus and which does not appear to have been adequately described in the literature. So far as can be gathered, this structure corresponds with the "inferior accessory process" of Sharp (1890) and the "genital embracer" of Yang (1938). A similar structure seems to be present in some other Heteroptera and it may be of general occurrence. It consists of a pair of curved arms, one on each side, with a common origin in the posterior margin of the ninth segment, the two arms curve around the aedeagus and are attached by membrane to the basal plate (fig. 12). At the common origin each arm

sends down a short branch which is fused to the ventral surface of the ninth segment. In the Oriental species, each arm at this point also sends up a vertical process, the two vertical processes being fused at the base but free apically, their shape providing excellent specific characters; fig. 12 shows the arrangement in lateral view, figs. 11 and 44-59 the appearance in terminal view. As the whole structure is fairly rigid, the aedeagus can move freely in an antero-posterior plane, but is probably prevented from twisting laterally. The aedeagus, when it is everted, apparently rides between the vertical processes and it is possible that they act as an additional guide. I propose for the purposes of this paper to name the vertical processes the "vertical processes of the ninth segment."

The parameres are variously shaped and are described in the following section under each group.

GROUPING AND SEPARATION OF THE SPECIES OF *Dysdercus* BOISDUVAL (EXCLUDING AMERICAN SPECIES).

The species fall into two groups on the presence or absence of vertical processes of the ninth segment: in all the Ethiopian species except *D. festivus* Gerstaecker—an East African species—they are absent, in all the Oriental species and *D. festivus* they are present.

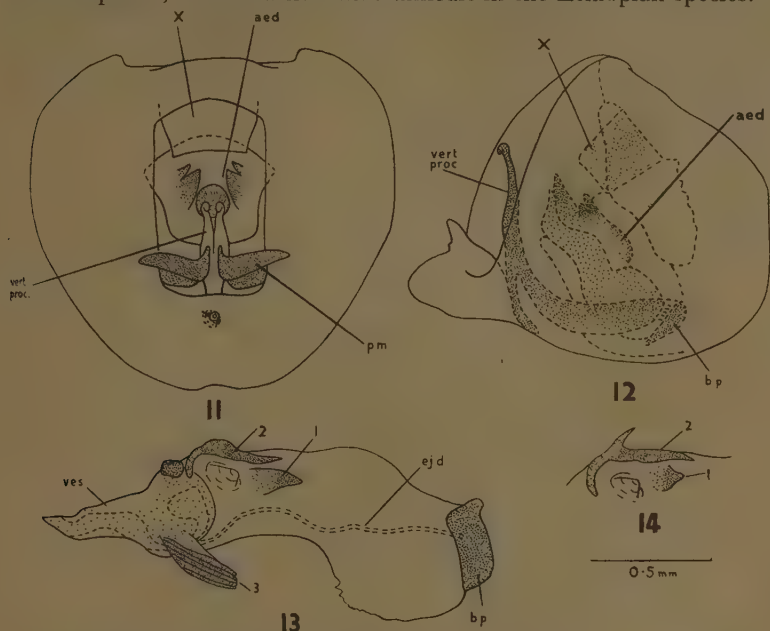


FIGS. 7-10. —Dorsal view of head and thorax of (7) *D. cingulatus* (Fabricius); (8) *D. olivaceus* (Fabricius); (9) *D. poecilus* (Herrich-Schäffer); (10) *D. decussatus* Boisduval.

The Oriental species (including *D. festivus*) can then be divided into two groups on the structure of the second conjunctiva appendage of the aedeagus and the shape of the spermatheca; this separation is confirmed by the shape of the prothorax and the punctuation of the scutellum. The final definition of each Oriental species depends on the shape of the vertical processes and parameres. The shape of the parameres is not always different for each species, but it can be used as a subsidiary method of grouping species within the major groups; there is some overlap between some of the subgroups, which may show evolution of the groups or may be due to some genetic factor.

The Ethiopian group can be separated into two subgroups on the structure of the ninth segment of the male and the spermatheca, this separation agreeing well with paramere structure. The final definition of species on paramere shape alone is not, unfortunately, always certain in closely allied species, and must be supplemented by colour characters.

It will be appreciated that definition of species is firmer for the Oriental species because of the extra character in the male genitalia. Using this extra character it is possible to assign colour forms to their correct species, a task rather more difficult in the Ethiopian species.



FIGS. 11-14.—(11) Postero-dorsal view of ninth segment of male of *D. sidar* Montrouzier (12) lateral view of the same, parameres removed; (13) lateral view of everted aedeagus of *D. koenigii* (Fabricius); (14) lateral view of first and second conjunctiva appendages of *D. decussatus* Boisduval. Degree of shading shows degree of sclerotisation. 1, 2, 3, first, second and third conjunctiva appendages; aed, aedeagus; b p., basal plate; ej. d, ejaculatory duct; pm, paramere; vert. proc, vertical processes of ninth segment; ves, vesica; X, tenth segment.

However, it has been shown by Vrydagh (1942) in his experiments with *D. nigrofasciatus* and *D. melanoderes* Karsch that these two species are true species though the main separating characters are ones of colour. He has shown that the biology of these two closely related species is different and that their habitats (except for cotton fields) are different. On the other hand, they will breed together to give viable and fertile hybrids, but the fertility rate is lower than usual; the offspring of these crosses on the whole are intermediate, though some new forms were produced; intermediates can be found in the cotton fields and possibly account for the extreme forms mentioned in the specific description below. In general his evidence suggests that the two species are closely allied but distinct, especially as the overlap in their distribution does not prevent their retaining their typical "specific" characters. Lamborn (1914 : 202) found a female *D. melanoderes* copulating with a male *D. superstiosus* (Fabricius) and he obtained eleven adults of the F_1 generation, but does not state whether they were fertile or not. Golding

(1928) was unable to confirm these results. If this interbreeding took place regularly in the field, one would imagine that specific boundaries would break down, because although the distribution of these species is not the same there are wide areas of overlap. The species seem to remain clear cut, however, even though, as Mr. Pearson informs me, *D. nigrofasciatus* and *D. superstitiosus* are often to be found feeding together on the same plant, and they must remain as true species until there is much more convincing evidence to the contrary.

The grouping may be shown as follows:—

I. Those species with no vertical processes of the ninth segment—
Ethiopian species.

I (a) Group of *D. superstitiosus* (Fabricius); those species with apex of ninth segment rounded; spermatheca with no separate accessory gland (fig. 15), duct wide and comparatively short, probably itself glandular. *D. superstitiosus* (Fabricius), *nigrofasciatus* Stål, *melanoderes* Karsch, *ortus* Distant, *flavidus* Signoret, *fasciatus* Signoret, *cardinalis* Gerstaecker.

I (b) Group of *D. intermedius* Distant; those species with apex of ninth segment conical; spermathecal duct very long and coiled, accessory gland present, usually recurved (fig. 16). *D. intermedius* Distant, *orientalis* Schouteden, *pretiosus* Distant, *haemorrhoidalis* Signoret.

II. Those species with vertical processes of ninth segment present—
Oriental species and *D. festivus*.

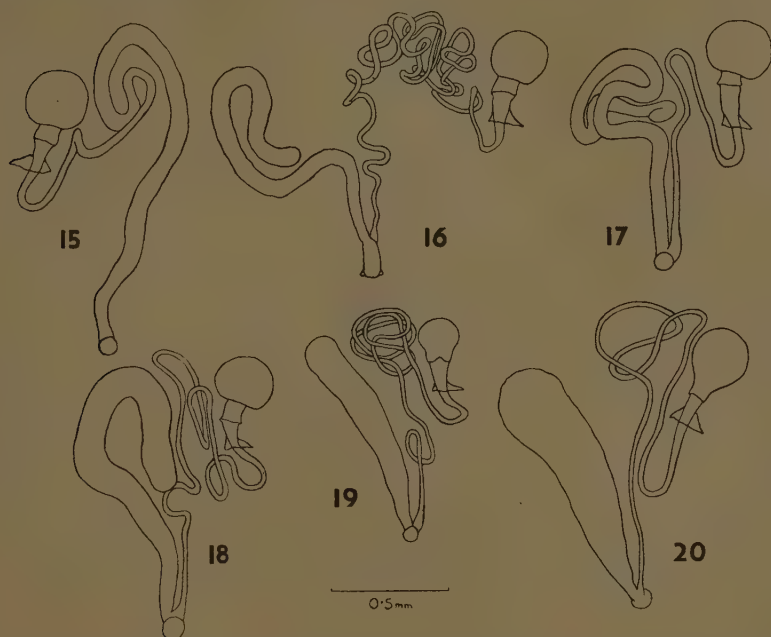
II (a) Group of *D. koenigii* (Fabricius); those species with second conjunctiva appendages of aedeagus simple; spermatheca globular, duct short or very short, accessory gland recurved or more or less coiled (figs. 17–18). *D. koenigii* (Fabricius), *solenis* (Herrich-Schäffer), *evanescens* Distant, *olivaceus* (Fabricius), *similis* sp.n., *poecilus* (Herrich-Schäffer), *transversalis* Blöte, *concinulus* Walker, *festivus* Gerstaecker, *cingulatus* (Fabricius), *sidæ* Montrouzier, *longiceps* Breddin.

II (b) Group of *D. decussatus* Boisduval; those species with second conjunctiva appendages forked; spermatheca more or less pear-shaped, duct fairly short, accessory gland simple more or less swollen apically (figs. 19–20). *D. argillaceus* Bergroth, *oceanicus* Boisduval, *mesostigma* Distant, *philippinus* Herrich-Schäffer, *decussatus* Boisduval.

Group of *D. superstitiosus*.

The parameres of these species have a double-hooked head (figs. 27–32), with the hooks projecting backwards over the rim of the ninth segment. There are two species, *D. fasciatus* and *cardinalis*, which are tolerably distinct and readily distinguished by the structure of the parameres and ninth segment. The other five species are closely allied and cannot be separated at all readily by paramere structure but fairly readily by colour characters; each has a definite range but there is

much overlap, particularly by *D. superstitiosus*. The nymphs of *D. cardinalis*, I am informed by Mr. Pearson, have the last antennal segment basally white—a common character in American species but not found elsewhere in Ethiopian species so far as I am aware. The spermatheca of the species of this group is peculiar in that the accessory gland is absent but the spermathecal duct is enlarged and appears to be glandular itself.



FIGS. 15–20.—Cuticular lining of spermatheca and accessory gland. (15) *D. superstitiosus* (Fabricius); (16) *D. intermedius* Distant; (17) *D. koenigii* (Fabricius); (18) *D. cingulatus* (Fabricius); (19) *D. decussatus* Boisduval; (20) *D. mesiostigma* Distant.

Group of *D. intermedius*.

Both the parameres and the ninth segment are of a strange and quite characteristic form. The parameres (figs. 34–37) bear an apical hook lying in a transverse plane and an outwardly directed process half-way along their length; the apical hook does not project over the rim of the ninth segment. *D. pretiosus* and *haemorrhoidalis* are closely allied and separable mainly by the presence or absence of spines along the length of the anterior femora; further information is required on the range and variability of these two species as the distinguishing characters are not in every way satisfactory. The other two species, *D. intermedius* and *orientalis*, are quite distinct. The spermathecal duct of the species of this group is much longer than in the species of the other groups.

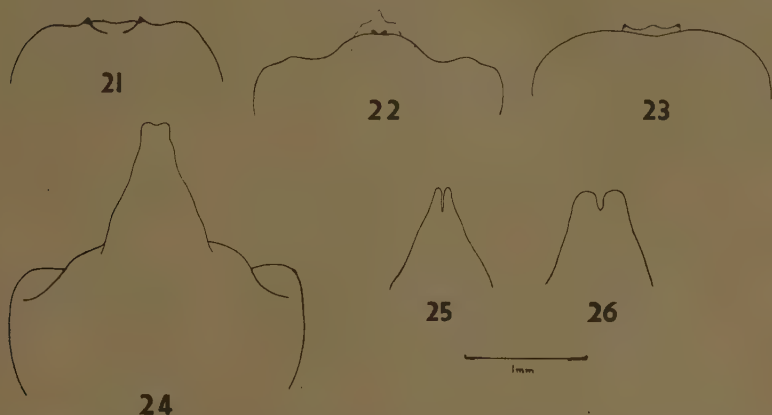
Group of *D. koenigii*.

The parameres are typically as shown in fig. 38, that is with the apex blunt and narrowly folded over and with a transverse crest terminating in a slight hook. The inner side is unarmed, it is the outer side which bears the crest; the hook points anteriorly and the parameres lie well inside the ninth segment. Most of the species possess parameres of this type and cannot be distinguished with any certainty using this character particularly as the exact shape is variable within a species. Those species which can be distinguished by paramere structure are *D. longiceps*, *cingulatus* and *sidæ*; in these species the parameres appear to have been derived from the typical *koenigii* type by an exaggeration or reduction of apical fold and crest. All species can be readily distinguished on the structure of the vertical processes of the ninth segment. With the exception of *D. festivus* and *longiceps*, this group is a complex of closely allied and variable species difficult to separate except by use of the male genital characters, a fact which accounts for the confusion which has existed in the past. The common, widespread Australo-Malayan species, extending to the eastern states of India, is *D. cingulatus* (*megalopygus* Breddin). Occurring within the range of this species are the five species *D. solenis* (Philippines, Borneo and Celebes), *D. evanescens* (India to Indo-China), *D. poecilus* (Assam to Malaysia), *D. transversalis* (Timor and neighbouring Is.) and *D. concinnulus* (*variegatus* Distant) (New Guinea, Gilolo); all are similar but may be distinguished by the characters given. The common Indian species, probably not occurring east of Bengal, is *D. koenigii* (*micropygus* Breddin); in general appearance it is almost identical with *D. cingulatus*, but, as first shown by Breddin, it can be easily separated by the male genitalia. Only *D. olivaceus* and *similis* (S. India and Ceylon) occur within its range and they, though similar to each other, can easily be separated from it. *D. sidæ* (*insularis* Stål) is quite a distinct species in its typical form, but some colour forms are difficult to separate from *D. cingulatus*; it has an Australasian and Pacific Is. distribution.

Group of *D. decussatus*.

This is a small group of species with a predominantly Australo-Malayan distribution, though *D. decussatus* and *mesio stigma* also occur in Ceylon and northwards into China and Formosa. The parameres show a transition from the *koenigii* type found in *D. oceanicus* and *argillaceus*, through an intermediate form shown by *D. mesio stigma* to an extreme form with exaggerated apical fold and much reduced crest shown by *D. decussatus* (figs. 42-43). *D. philippinus*, of which I have seen no males, probably resembles *D. decussatus* in this respect. *D. oceanicus* (*impictiventris* Stål) and *argillaceus* are allied and show a strong resemblance in the shape of vertical processes, but *argillaceus* has the apical segment of the antenna pale—a unique feature in adult non-American species so far described. *D. mesio stigma* and *decussatus* are similarly united in the shape of vertical processes and both have the lateral margins of the thorax strongly sinuate, but *mesio stigma* is unique in being pubescent over most of its surface and lacks the strong basal scutellar punctures of the other species of this group. Breddin (1900)

suggested that *mesio stigma* was sufficiently different from the other species to warrant inclusion in a separate subgenus *Megadysdercus*. Despite its differences, the similarity of both genitalia and thorax prevent its generic or subgeneric separation from *decussatus*, and, as *decussatus* is the genotype of *Dysdercus*, then the name *Megadysdercus* cannot stand. *D. decussatus* is a very variable species and its various forms have in the past been considered to be true species; in colour there is a complete transition from forms with a white cross on a red background, to practically all black forms, and as many "species" as desired can be described using colour characters.



FIGS. 21-26.—Ninth segment of males: 21-23 postero-ventral view, 24-26 ventral view. (21) *D. nigrofasciatus* Stål; (22) *D. fasciatus* Signoret; (23) *D. cardinalis* Gerstaecker; (24) *D. intermedius* Distant; (25) *D. orientalis* Schouteden, apex only; (26) *D. pretiosus* Distant, apex only.

The four following species, included in Hussey's Catalogue (1929), I have found to be quite unrecognisable and I have seen no specimens at all resembling the descriptions:—

D. coloratus Walker, 1872. The type is lost, and the striking ventral pattern suggests that it is not a *Dysdercus*.

D. pyrrhomelas Herrich-Schäffer, 1843. From the figure it is probably not a *Dysdercus*.

Astemma sappho Kirkaldy and Edwards, 1902. The figure shows the apex of the wings to be broadened and rounded which prevents its inclusion in *Dysdercus*.

D. scassellatii Del Guercio, 1918. The description and figures suggest that it is not a *Dysdercus* because of the peculiar arming of the femora, the proportions of the femora and tibiae and the pattern of the thorax.

Hussey also mentions two other species, *D. migratorius* Distant and *D. antennatus* Distant. These two species and Hussey's *Dindymus flavipes* Signoret are all closely related. Blöte (1931: 117) states that

D. antennatus is a *Dindymus*, but it seems more likely that these three species with some other African species at present included in *Dindymus* are really generically distinct. It is quite certain from their general form, wing-venation, structure of the parameres and peculiar ventral pattern, that they do not belong to *Dysdercus*.

The considerable new synonymy introduced in this paper has, unfortunately, not always been founded on examination of types, but in nearly every case the original description was sufficient to identify the species. I have put a short note after each species with new synonymy, explaining my reasons.

The following types have been examined: *Cimex superstitiosus* Fabricius, *Dysdercus ortus* Distant, *D. intermedius* Distant, *D. pretiosus* Distant, *D. evanescens* Distant, *D. concinnulus* Walker, *D. simplex* (*variegatus*) Distant, *Cimex cingulatus* Fabricius, *Dindymus biguttatus* Walker, *Dysdercus albescens* Walker, *D. mesiostigma* Distant, *Dindymus simplex* Walker, *Dysdercus papuensis* Distant and a cotype of *D. remotus* Distant.

KEY TO THE ETHIOPIAN, ORIENTAL AND AUSTRALASIAN SPECIES OF
Dysdercus BOISDUVAL.

1. Vertical processes of ninth segment of male absent; African species 2
Vertical processes of ninth segment of male present; Oriental and Australasian species, except *D. festivus* 12
2. If corium fasciated then a black band present posteriorly on prothorax, either band may be absent in specimens from Madagascar, Mascarene or neighbouring islands; ninth segment of male rounded in ventral view 3
Corium clearly fasciated but posterior black band on prothorax always absent, species not from Eastern Islands; ninth segment of male conical 8
3. Prothoracic black band broad, reaching over on to disc (if band absent in some island varieties then head and rostrum elongate as in fig. 2) 4
Prothoracic black band narrow and linear, or if absent head not elongate (fig. 1) 5
4. Head elongate (fig. 2); posterior pronotal fascia a narrow ellipse absent in some island forms; scutellum reddish; anterior femora strongly spined along their length *fasciatus* Signoret
Head less elongate, posterior pronotal fascia suffusing much of the disc; scutellum blackish; anterior femora weakly spined along their length; species from Seychelles *ortus* Distant
5. Metathoracic scent gland spout red, usually clear red, but if suffused, never deep black; venter obviously patterned either with red or yellow and white; second segment clearly fasciated as in fig. 1 6
Scent gland spout deep black; venter less obviously patterned, never with red, second segment almost entirely white 7
6. Prothoracic black fascia clearly and distinctly defined; corial fascia formed by two broad black spots *superstitiosus* (Fabricius)
Prothoracic black fascia absent or ill-defined; corial fascia present or absent, but not in the form of two broad spots *flavidus* Signoret

7. Membrane always dark or black ; dorsal surface maculated
nigrofasciatus Stål
Membrane of hemelytra always pale ; dorsal surface usually but
not always immaculate, ochraceous, more yellow in maculated
forms *melanderes* Karsch
8. Ventral abdominal segments 1-4 mainly white, the red forming
a distinctive pattern of triangular spots on 3 and 4 (fig. 3)
cardinalis Gerstaecker
Pattern of venter different 9
9. Anterior pronotal callus and lateral margins black or partially
black *orientalis* Schouteden
Anterior pronotal callus and lateral margins red or yellow 10
10. Pattern of venter as in fig. 4, abdominal segments black along
their anterior margins *intermedius* Distant
Pattern of venter as in fig. 5, abdominal segments 1-3 with no
black anteriorly 11
11. Anterior femora strongly spinose along their length *pretiosus* Distant
Anterior femora with only the usual few spines subapically
haemorrhoidalis Signoret
12. Corial markings always in form of black spots or transverse lines,
except in *D. concinnulus* and some varieties of *D. poecilus*, in
which they are lacking ; scutellum never punctured or
pubescent ; second conjunctiva appendage of male simple 13
Corial markings never in the form of black spots or transverse lines,
often absent ; scutellum basally with strong sparse punctures or
scutellum and prothoracic fold finely pubescent ; second con-
junctiva appendage forked (fig. 14) 24
13. Corium immaculate ; first ventral segment with distinct white
fascia *concinnulus* Walker
Corial fascia usually present either as two black spots or two
lines ; when absent then first ventral abdominal segment lacking
a distinct white fascia 14
14. Corial spots touching or nearly touching inner margin ; corium
sometimes clouded but costal margin always pale ; if spots
absent then first (true) ventral segment with no white fascia 15
Corial spots placed centrally or touching both margins, or fascia
in form of two lines touching both margins, never absent ;
white fascia always present on first ventral segment 16
15. Corial spots circular, often large or corium largely infuscated,
may be missing, never transverse . . . *poecilus* (Herrich-Schäffer)
Corial spots elongate, linear . . . *transversalis* Blöte
16. Disc, posterior margin of prothorax and corium not all concolorous 17
Disc, posterior margin of prothorax and corium all more or less
concolorous 18
17. Prothorax with broad black band or ellipse posteriorly ; corium
uniformly coloured ; head elongate and swollen *longiceps* Breddin
Prothorax with no black band posteriorly ; corium broadly red or
yellow along the costal margin ; head normal, but eyes large
solenis Herrich-Schäffer
18. Membrane pale ; corial spots very small for size of insect
evanescens Distant
Membrane black 19
19. Thorax wider posteriorly (fig. 8) ; head red, usually clearly
different in colour from the ochraceous corium ; white ventral
abdominal fasciae sometimes bifid (fig. 6) ; species from S. India
and Ceylon 20

- Thorax narrower posteriorly (fig. 7); head red, but not clearly different from the orange corium; abdominal fasciae never bifid 21
20. White ventral fasciae varying from slightly to strongly bifid; vertical processes of ninth segment broad, transparent (fig. 46)
olivaceus (Fabricius)
White ventral fasciae sometimes very slightly bifid, never strongly so; vertical processes narrower, not transparent (fig. 47)
similis sp. n.
21. Rostrum longer, often reaching to apex of fourth segment; prothoracic white collar not crescentic, often narrow, reaching to anterior angles; segment 6 mainly dark or black, venter often mainly pale, usually with no red; parameres as fig. 40
sidæ Montrouzier
Rostrum usually reaching second segment but sometimes base of third; prothoracic white collar more or less absent, or strongly crescentic, rarely reaching angles; segment 6 not dark or black; venter never mainly pale, nearly always red with white fasciae 22
22. Corial fascia a narrow black line touching both margins; African species
Corial fascia in form of two black spots, when touching both margins not narrow; Oriental species 23
festivus Gerstaecker
23. Femora red, only very occasionally dark; parameres as fig. 38; spermatheca duct short, accessory gland more coiled (fig. 17); species from India and Ceylon
koenigii (Fabricius)
Femora usually at least apically dark; parameres as fig. 39; spermatheca duct longer, accessory gland thicker and simpler (fig. 18); species from Assam eastwards to Malaysia, S. China and Australasia
cingulatus (Fabricius)
24. Membrane light with black spot basally across anal angle; prothoracic fold and scutellum finely pubescent
mesiotigma Distant
Membrane uniformly dark; no pubescence on dorsal surface; scutellum with strong but not close punctures basally 25
25. Clavus and corium uniformly grey, no trace of St. Andrew's cross on coria; scutellum red or yellow; vertical processes as in figs. 56 and 57 26
- Clavus dark or black, not always concolorous with corium which may be red, grey or black, usually at least a trace of St. Andrew's cross on coria; scutellum normally dark or black; vertical processes as in fig. 59 (those of *D. philippinus* may be different) 27
26. Apical antennal segment pale yellowish; ventral abdominal segments 2-6 with red and white or red and grey fasciae
argillaceus Bergroth
Apical antennal segment dark or black; ventral segments 2-6 either completely flushed with red or else venter yellow with red abdominal margins and apex
oceanicus Boisduval
27. Anterior femora bearing spines subapically only, not thicker than hind femora; posterior arms of white corial cross strongly widened to margin; larger species
philippinus Herrich-Schäffer
Anterior femora bearing spines along their length ventrally, thicker than hind femora; posterior arms of cross (when present) not strongly widened to margin; smaller species
decussatus Boisduval

Dysdercus supersticiosus (Fabricius, 1775).

supersticiosus Fabricius, 1775 : 719 (*Cimex*). Goeze, 1778 : 256 (*Cimex*). Fabricius, 1781 : 364 and 1787 : 299 (*Cimex*). Thunberg, 1784 : 55 (*Cimex*). Gmelin, 1788 : 2171 (*Cimex*). Fabricius, 1794 : 153 and 1803 : 221 (*Lygaeus*). Signoret, 1858 : 307 (*Dysdercus*). Stål, 1866 : 15, 1868 : 84 and 1870 : 118 (*Dysdercus*). Lethierry, 1883b : 749 (*Dysdercus*). Distant, 1884 : 461 (*Dysdercus*). Gerstaecker, 1891 : 50 (*Dysdercus*). Bergroth, 1894 : 358 (*Dysdercus*). Karsch, 1894 : 106 (*Dysdercus*). Haglund, 1895 : 467 (*Dysdercus*). Distant, 1902b : pl. xix, fig. 50 (*Dysdercus*). Schouteden, 1905 : 10 and 16 (*Dysdercus*). Schouteden, 1912 : 304 and 305 excl. vars. (*Dysdercus*). Schumacher, 1912 : 319 (*Dysdercus*). Courteaux, 1922 : 286 (*Dysdercus*). Bergroth, 1926 : 12 (*Dysdercus*). Hussey, 1929 : 103 excl. vars *nigriceps* and *tergiversans* (*Dysdercus*). Blöte, 1931 : 132 (*Dysdercus*). Schmidt, 1932 : 275 (*Dysdercus*).
capensis Wolff, 1802 : 107 (as var. of *Lygaeus koenigii*).
albicollis Schaum, 1862 : 45 (*Pyrrhocoris*).
volkeri Schmidt, 1932 : 275 (*Dysdercus*), syn. nov.

Antennae : First segment clearly longer than the second, but not subequal to two and three together. *Rostrum* : Reaches second abdominal segment, proportions of segments normal. *Anterior femora* : Besides the usual subapical spines, there are indications of small spines along their lengths ventrally (compare *nigrofasciatus*). *Male genitalia* : Ninth segment apically with two small conical teeth and a depression between—as in all species of this group (fig. 21). *Parameres* (fig. 27) with apex always rounded, never flat though rather variable. *Spermatheca* : No accessory gland, duct wide (fig. 15).

Colour of dorsal surface : Head red or yellow, usually dark posteriorly. *Prothorax* with white collar, fold and lateral margins concolorous with head, disc yellowish-grey, posterior margin with narrow black fascia, though margin itself very narrowly pale. *Scutellum* yellow or reddish. *Corium* yellowish-grey, often outlined with yellow ; black fascia present as a pair of large oval spots, normally not touching margins, but they may be reduced to narrow rectangles or enlarged to touch inner and outer margins quite broadly. *Membrane* very dark.

Colour of ventral surface : Typically clear red and white with pattern as shown in fig. 1, with no trace of black, but red sometimes becomes darkened and blackish on pleurites of thorax and abdominal segments ; yellow forms occur as described below ; second abdominal segment with white confined to a posterior fascia (compare *nigrofasciatus*) ; white fasciae narrowed centrally. Metathoracic scent gland spout usually clear red, but may be darkened in dark forms, never deep black as in *nigrofasciatus*. Narrow black streaks never present anteriorly on abdominal segments ; red and white (or yellow and white) pattern always distinct.

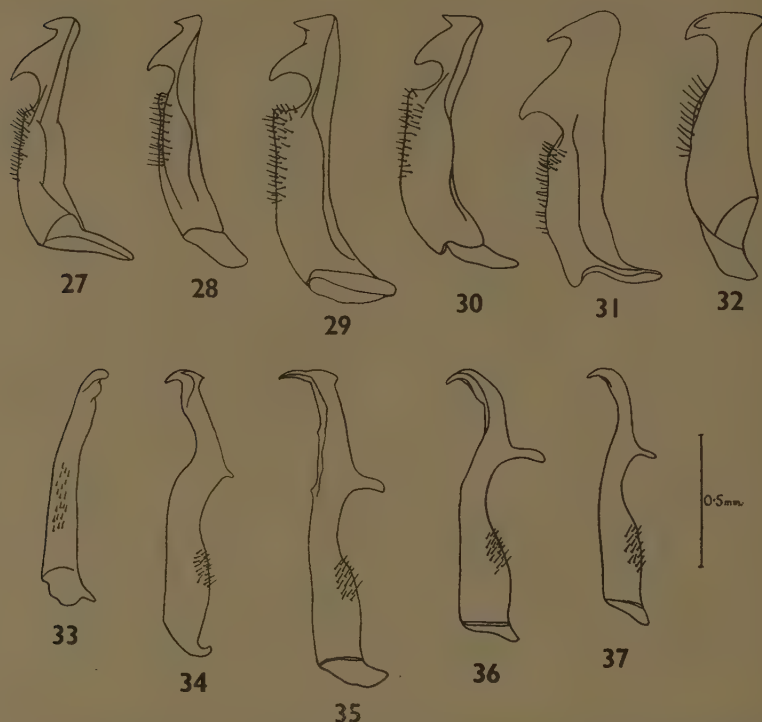
Legs : Coxae, trochanters and femora usually red, but femora may be dark ; tibiae and tarsi variable but usually red suffused with black.

Length 12–17.5 mm., *breadth across wings* 3.5–6 mm.

A fairly large species with distinctly patterned venter, scent gland spout at least partially red, a black fascia on pronotum and usually oval spots forming corial fascia.

Colour Variation.

The majority of specimens show a red coloration on the ventral surface and elsewhere. A few, however, have the red replaced by yellow but still retain an obviously patterned venter. Golding (1925 and 1928) discovered that these yellow forms were common and dominant early in the season, but that they were gradually replaced by red forms as the season wore on. He also found that the corial fasciae varied, “banded” and “spotted” forms, which did not interbreed, being produced. Further investigation may throw more light on this problem, but from the point of view of this paper I can do little but draw attention to its existence, as few of the Museum specimens have accurate dates. It is possible that this type of variation exists in other species.



FIGS. 27-37.—Lateral view of right parameres of Ethiopian species. (27) *D. superstitiosus* (Fabricius); (28) *D. nigrofasciatus* Stål; (29) *D. melanoderes* Karsch; (30) *D. ortus* Distant; (31) *D. fasciatus* Signoret; (32) *D. cardinalis* Gerstaecker; (33) *D. festivus* Gerstaecker; (34) *D. intermedius* Distant; (35) *D. orientalis* Schouteden; (36) *D. pretiosus* Distant; (37) *D. haemorrhoidalis* Signoret.

The type, a male, is in the Banks Collection in the British Museum (Natural History).

Distribution of specimens seen: GAMBIA: 3 ♂, 2 ♀, iv.1911 (*J. J. Simpson*). SIERRA LEONE: Yana, 2 ♂, 1 ♀, iii.1912 (*J. J. Simpson*); Imadu, 1 ♂, vi.1912 (*J. J. Simpson*); Daru, 1 ♂, viii.1912 (*J. J. Simpson*); Bo, 1 ♂, ix.1912 (*J. J. Simpson*); no details, 1 ♀, vi.1917 (*P. A. Buxton*); Segbwema, 2 ♂, 4 ♀, 1.1925 (*E. Hargreaves*); Bohol, 3 ♂, v.1925 (*E. Hargreaves*). IVORY COAST: Beoumi, 1 ♀, xi.1922 (*Lowe and Hardy*). ASHANTI: Krachi, 2 ♂, 2 ♀, ii.1927 (*J. J. Simpson*); Coomassie, 1 ♀ (*N. Samwell*). GOLD COAST: 1 ♂, 3 ♀, ii.1911 (*L. Armstrong*); Battou, 1 ♀, x.1911 (*H. T. Palmer*); Kona, 1 ♀, i.1913 (*J. J. Simpson*); Yapi, 21 ♂, 26 ♀, xii.1916 (*J. J. Simpson*); Tamale, 1 ♂, 3 ♀, xii.1916 (*J. J. Simpson*); Aburi, 3 ♂, 3 ♀ (*W. H. Patterson*); 2 ♀ (*A. R. Gould*). DAHOMEY: Cotonou, 1 ♂, 4 ♀, v.1914 (*W. A. Lamborn*); Sagranga, 1 ♀, i.1917 (*J. J. Simpson*). NIGERIA: Oshogbu, 3 ♀, ii.1910 (*J. J. Simpson*); Meko, 1 ♂, ii.1910 (*J. J. Simpson*); Ato, 1 ♀, ii.1910 (*J. J. Simpson*).

Simpson); Benin City, 2 ♂, 2 ♀, iii.1910 (*J. J. Simpson*); Onitsha, 1 ♀, vii.1910 (*J. de Gaye*); Baro, 2 ♂, 2 ♀, x.1910 (*J. J. Simpson*); Bokani, 2 ♀, x.1910 (*J. J. Simpson*); 1 ♂, xii.1910 (*C. E. S. Watson*); Dekina, 1 ♀, i.1911 (*Scott-Macfie*); Ibadan, 29 ♂, 39 ♀, i-iii.1923 (*A. W. J. Pomeroy*); Ibadan, 5 ♂, 3 ♀ (*J. Currie*); Azare, 8 ♂, 5 ♀, 1924 (*Ll. Lloyd*); Gadau, 1 ♂, 1 ♀, vi.1933 (*Buxton and Lewis*); Panyam, 1 ♀ (*G. T. Fox*); Lagos, 4 ♂, 4 ♀; S. Nigeria, 5 ♂, 4 ♀. PRINCIPE I.: 1 ♂, xii.1932 (*W. H. T. Tams*). CAMEROONS: Badere, 1 ♂, iv.1914; Dendeng, 2 ♂, 3 ♀, iv.1914; Betare, 1 ♂, iv.1914; Kongola, 1 ♀, iv.1914; Buar, 5 ♂, 4 ♀, v.1914; Babua Bondaye, 2 ♂, 2 ♀, v.1914; Batouri District, 1 ♀, ii.1936 (*F. G. Merfield*); Escalera, 3 ♂, 2 ♀; Jaunde, 2 ♀. BELGIAN CONGO: Lualaba R., 4 ♂, 5 ♀, iv.1907 (*S. A. N.*); Kambove, 3 ♂, x.1907 (*S. A. N.*); Bangala District, 1 ♀, ii.1922 (*L. Jenniaux*); Isubu, 3 ♂, 1 ♀; Ituri, 1 ♀. S.W. AFRICA: Okahandja, 1 ♀, iii.1928 (*R. E. Turner*); Hoffnung, 1 ♂, 1 ♀, i.1934 (*K. Jordan*). BECHUANALAND: Ghanzi, 3 ♀, iii.1926 and 1 ♂, ix.1926 (*J. Maurice*); Palapye, 1 ♀, iii.1934 (*J. Ogilvie*). S. RHODESIA: Salisbury, 1 ♀, i.1906 (*G. A. K. Marshall*) and 1 ♂, 2 ♀. N. RHODESIA: L. Bangweolo, 1 ♀; no details, 1 ♀. NYASALAND: 1 ♀ (*J. E. S. Old*). TANGANYIKA: Usanga District, 1 ♂, 1 ♀, xii.1910 (*S. A. N.*); Ruaha R., 2 ♀, xii.1910 (*S. A. N.*); Niomkolo, 2 ♂, 1 ♀; Lulanguru, 1 ♀, xi.1917 (*G. D. H. Carpenter*); no details, 1 ♀ (*A. Loveridge*), 1 ♀ (*W. H. Nutt*). KENYA: Mt. Kenya, 1 ♂, ii.1911 (*S. A. N.*); Naivasha, 1 ♂, iii.1911 (*S. A. N.*); Mumias, 1 ♂, vi.1911 (*S. A. N.*); Kavirondo, 1 ♂, vi.1911 (*S. A. N.*); Trans-Nzoia, 3 ♂, 1 ♀, vii.1926 (*C. R. S. Pitman*); Kinjabe, 1 ♂, 2 ♀ (*C. S. Betton*); Njoro, 1 ♀ (*A. J. Chalmley*). UGANDA: Msozi, 6 ♀, ii.1903 (*Delme-Radcliffe*); Mbale District, 4 ♂, 6 ♀, viii.1911 (*S. A. N.*); Unyoro, 1 ♂, 4 ♀, xii.1911 (*S. A. N.*); Entebbe, 5 ♀, xii.1912 (*C. C. Gowdey*); Semliki Plains, 1 ♀ (*S. A. N.*). ABYSSINIA: Higo Samula, 1 ♂, x.1911 (*R. J. Stordy*); Alaba, 1 ♂, 1 ♀, xi.1911 (*R. J. Stordy*); L. Zwai, 1 ♀, v.1914 (*O. Kovacs*); Maraquo, 1 ♂, 3 ♀, vii.1914 (*O. Kovacs*); Addis Allem, 1 ♂, ix.1926 (*H. Scott*); Doukham, 4 ♂, 2 ♀, x.1926 (*H. Scott*); Mt. Zuquala, 5 ♂, 1 ♀, x.1926 (*H. Scott*); Addas, 1 ♂, 2 ♀, xi.1926 (*Omer Cooper*); Shoa, L. Cialalaka, 1 ♂, 1 ♀. ANGLO-EGYPTIAN SUDAN: Tokar, 2 ♂, iii.1926 (*H. H. King*); no details, 2 ♂, xi.1917 (*J. R. Yardley*); Upper Nile, 2 ♂, 4 ♀ (*W. B. Drury*).

Type locality, America (presumably in error).

An account of the biology of this species is given by Pomeroy and Golding (1923) and Golding (1925 and 1928).

Dysdercus nigrofasciatus Stål, 1855.

- nigrofasciatus* Stål, 1855: 36 (*Dysdercus*). Stål, 1866: 14 and 1870: 118 (*Dysdercus*). Distant, 1902b: pl. xix, fig. 49 and 1909b: 79 (*Dysdercus*). Schouteden, 1910: 153 and 1912: 303 and 305 (*Dysdercus*). Distant, 1913: 158 (*Dysdercus*). Heymons, 1915: 147 (*Dysdercus*). Courteaux, 1922: 286 (*Dysdercus*). Bergroth, 1926: 12 (*Dysdercus*). Hussey, 1929: 96 (*Dysdercus*). Blöte, 1931: 129 (*Dysdercus*).
superstitiosus Bergroth, 1894: 358 in part (*Dysdercus*).
intermedius (nec Distant) Schouteden, 1910: 154 (as var. of *D. nigrofasciatus*).
nigriceps Schouteden, 1910: 154 (as var. of *D. nigrofasciatus*). Schouteden, 1912: 303 (as var. of *D. superstitiosus*). Hussey, 1929: 104 (as var. of *D. superstitiosus*).
tergiversans Hussey, 1929: 104 (as var. of *D. superstitiosus*, nom. nov. pro var. *intermedius* Schouteden, 1910), syn. nov.
nigrescens Vrydagh, 1942: 24 (as var. of *D. nigrofasciatus*).

Antennae : First segment clearly longer than the second, but not subequal to two and three together. *Rostrum* : Reaches second abdominal segment, proportions of segments normal. *Anterior femora* : Besides the usual subapical group of spines, there are distinct though small spines along their length ventrally (compare *superstitiosus*). *Male genitalia* : Ninth segment (fig. 21) with two small conical teeth and a depression between. Parameres (fig. 28) of *superstitiosus* type but apex definitely flat and more or less pointed anteriorly—less robust than in *melanoderes*. *Spermatheca* : Duct wide, accessory gland absent (fig. 15).

Colour of dorsal surface : Head varying from black (Schouteden's and Vrydagh's vars.) to clear yellow, a complete series can readily be found ; posterior margin always dark brown or black. *Prothorax* with white collar, fold and lateral margins yellow or red, posterior margin with narrow black fascia (margin itself very narrowly pale), disc yellowish-grey. *Scutellum* yellowish-grey. *Corium* usually yellowish-grey, but exact shade variable and both grey and yellow forms occur ; usual black fascia present in form of narrow parallel-sided stripe which may or may not reach margins and is variable in width. *Membrane* very dark.

Colour of ventral surface : Pattern in general similar to that of *superstitiosus* (fig. 1) but easily distinguished because second abdominal segment almost completely white ; red of *superstitiosus* replaced by light yellow not clearly distinguishable from white, giving at first glance an appearance of uniform light yellow venter ; segments 5 and 6 often orange. Readily distinguished from all its allies except *melanoderes* by distribution of black as follows : spout of metathoracic scent gland and anterior margins of meso- and metathorax deep black ; each abdominal segment narrowly black along anterior margin laterally which accentuates segment junctions.

Legs : Coxae, trochanters and femora usually red, tibiae and tarsi usually dark ; femora may be darkened also.

Length 11.5–18 mm., *breadth across wings* 4.6–5 mm.

A fairly large species with two narrow black fasciae, dark membrane, deep black scent gland, pale venter with black incisures and white second segment.

I have not seen the type.

Distribution of specimens seen : ANGLO-EGYPTIAN SUDAN : Dinder R., Blue Nile, 1 ♂, 1 ♀, vii.1907 (*S. S. Flower*) ; Nuba Mts., Talodi, 1 ♂, xi.1921 (*F. Moysey*). ABYSSINIA : Shoa, L. Cialalaka, 2 ♂, 2 ♀, vii.1878 (*Antinori*) ; Wooromon, 1 ♀, iv.1904 (*C. Singer*) ; Addis Ababa, 1 ♂, 1 ♀, xi.1911 (*R. J. Stordy*) ; Alaba, 1 ♂, xi.1911 (*R. J. Stordy*) ; Maraco, 5 ♂, 4 ♀, iv.1914 (*O. Kovacs*) ; L. Zwai, 12 ♂, 11 ♀, v.1914 (*O. Kovacs*) ; Horadaka, 1 ♂, 3 ♀, vi.1914 (*O. Kovacs*) ; Maraquo, 19 ♂, 15 ♀, vii.1914 (*O. Kovacs*) ; Doukham, 2 ♂, 5 ♀, x.1926 (*H. Scott*) ; Addas, 1 ♂, 1 ♀, xii.1926 (*H. Scott*). KENYA : various localities and collectors too numerous to record, 83 ♂, 82 ♀. UGANDA : as for Kenya, 125 ♂, 146 ♀. TANGANYIKA : Bukoba, 1 ♂, 2 ♀, vi.1912 (*C. C. Gowdey*) and 3 ♂, iv.1916 (*A. Loveridge*) ; Noisinak Bridge, 1 ♂, v.1916 (*W. A. Lamborn*) ; L. Manyara, 2 ♂, 2 ♀, 1937 (*B. Cooper*) ; no details, 2 ♂, 2 ♀ (*A. Loveridge*). CAMEROONS : Batouri District, 2 ♀, v.1935 and 1 ♀, i–ii.1936 (*F. G. Merfield*) ; Abong M'Bang District, 1 ♀, iv.1936 (*F. G. Merfield*). BELGIAN CONGO : Mayumbe, 1 ♂, xii.1915 (*R. Mayne*) ; Ruanda, 1 ♂, 2 ♀ (*C. H. Marshall*). N. RHODESIA : Petauke, 1 ♀, ix.1910 (*S. A. N.*) ; L. Bangweolo, 1 ♀. NYASALAND : Chiromo, 2 ♂, 1 ♀, iv.1910 (*S. A. N.*) ; Shire V., 2 ♂, iv.1910 (*S. A. N.*) ; Blantyre, 1 ♂, vi.1910 (*J. E. S. Old*) ; Karonga, 2 ♂, 3 ♀, vii.1910 (*S. A. N.*) ; Mlanje, 2 ♂, i.1914 (*J. B. Davey*) ;

Zomba, 2 ♂, 2 ♀ (*H. H. Stannus*); no details, 2 ♀. PORTUGUESE EAST AFRICA: Chirinda Forest, Gaza Land, 1 ♀, iii.1907 (*D. Odendaal*; Mt. Chiperrone, 3 ♂, xi.1913 (*S. A. N.*). TRANSVAAL: Barberton, 1 ♀; Pretoria, 1 ♀. NATAL: Pt. Shepstone, 1 ♂, 4 ♀; Howick, 4 ♂, 2 ♀; Estcourt, 1 ♂, 1 ♀; Durban, 5 ♂, 4 ♀; Zululand, 1 ♀; Karkloof, 3 ♂, 1 ♀; Malvern, 1 ♂, 2 ♀. CAPE PROVINCE: Pt. St. John, 7 ♂. iv.1923 (*R. E. Turner*); no details, 1 ♀.

Type locality, Natal.

Accounts of the biology of this species are given by Ulyett (1930) and Vrydagh (1942).

Dysdercus melanoderes Karsch, 1892.

melanoderes Karsch, 1892: 133 (*Dysdercus*). Karsch, 1894: 106 (*Dysdercus*). Haglund, 1895: 467 (*Dysdercus*). Distant, 1902b: 42 (*Dysdercus*). Schouteden, 1912: 303 and 305 (*Dysdercus*). Hussey, 1929: 94 (*Dysdercus*). Blöte, 1931: 128 (*Dysdercus*). Schmidt, 1932: 277 (*Dysdercus*).

nigrofasciatus var. (b) Stål, 1866: 15 (*Dysdercus*).

Antennae: First segment clearly longer than second, often nearly as long as two and three together. *Rostrum*: Reaches second abdominal segment or occasionally base of third; proportions of segments normal. *Anterior femora*: Usually with distinct but small spines along their length as in *nigrofasciatus*, but occasionally almost spineless, except subapically. *Male genitalia*: Ninth segment as in *nigrofasciatus* (fig. 21). Parameres (fig. 29) of *superstitiosus* type, apex definitely flat but longer than in *nigrofasciatus*. *Spermatheca*: Duct wide, accessory gland absent (fig. 15).

Colour of dorsal surface: Typically uniformly ochraceous with white pronotal collar. Specimens of an extreme form occur showing a narrow black fascia on the posterior margin of the prothorax and a corial fascia formed by two elongate black spots not reaching either margin; in this form, head yellow, prothoracic and lateral margins broadly orange yellow, scutellum yellow, corium outlined by yellow, disc of corium and pronotum grey ochraceous. Intermediates between these forms do occur. *Membrane* much paler than in any other species, a character which readily separates it, even in the extreme form, from *D. nigrofasciatus* Stål.

Colour of ventral surface: Uniformly ochraceous in typical form with indications of usual white areas on thorax; abdominal segments narrowly black along anterior margins. Metathoracic scent gland spout and anterior margins of meso- and meta-pleurites black. The banded form has orange yellow anterior margins to abdominal segments which with white posterior margins produce a pattern as in *nigrofasciatus*; fifth and sixth segments mainly orange yellow with black anterior margin sometimes produced backwards as a large triangular spot each side; thoracic black suffusions along anterior margins larger and white margins more pronounced.

Legs: Femora pale, tibiae and tarsi usually dark.

Length 15–22 mm., *breadth across wings* 5–8 mm.

A large, broad, light coloured species with margins of thorax usually broadly upturned.

I have not seen the type.

Distribution of specimens seen: ASHANTI: Bompata, 2 ♂ (*A. E. Evans*); Ojesu, 1 ♂ (*A. E. Evans*). NIGERIA: Olofat, 1903, 1 ♀ (*Annett*); Aba, 1 ♂, v.1910 (*J. J. Simpson*); Oni R., 1 ♂, 1 ♀ xii.1910 (*W. A. Lamborn*); Lagos, 1 ♀, i.1911 (*W. A. Lamborn*); Ibadan, 1 ♂, vii.1922 (*F. D. Golding*); and 18 ♂, 10 ♀, i–iii.1923 (*W. J. Pomeroy*); Old

Calabar, 1 ♀. CAMEROONS : Escalera, 1 ♂, 4 ♀, 1903 ; Victoria, 1 ♀, 1916 (*F. H. Fitzroy*) ; Abong M'Bang, 1 ♀, iv.1934. BELGIAN CONGO : Isubu, 1 ♂ ; Mongo-ma-Lobah, 1 ♂. ANGOLA : Congulu, 3 ♂, 7 ♀, iv.1934 (*K. Jordan*) ; no details, 1 ♀. PRINCEPE I. : 1 ♂, 1 ♀, xii.1932 (*W. H. T. Tams*).

Type locality : L. Barombi, S. Cameroons, Nigeria.

An account of the biology of this species is given by Vrydagh (1942).

Dysdercus flavidus Signoret, 1861.

flavidus Signoret, 1861 : 955 (*Dysdercus*). Stål, 1866 : 16 and 1870 : 119 (*Dysdercus*). Lethierry, 1883 : 749 (*Dysdercus*). Reuter, 1887 : 93 (*Dysdercus*). Schouteden, 1912 : 305 (*Dysdercus*). Courteaux, 1922 : 286 (*Dysdercus*) ? China, 1924 : 436 (*Dysdercus*). Hussey, 1929 : 90 (*Dysdercus*). Blöte, 1931 : 121 (*Dysdercus*). Schmidt, 1932 : 277 (*Dysdercus*).

fasciatus (nec Signoret) Butler, 1879 : 550 (*Dysdercus*).

immaculatus Schmidt, 1932 : 277 (as var. of *D. flavidus*).

Antennae : First segment clearly longer than the second, but not as long as two and three together. *Rostrum* : Longer than usual, reaching to third abdominal segment at least, often just to the base of fourth ; proportions of segments normal or third segment slightly longer than fourth. *Anterior femora* : As in *nigrofasciatus* with distinct small spines besides the sub-apical group. *Male genitalia* : Ninth segment similar to that of *nigrofasciatus* (fig. 21). Parameres difficult to distinguish with certainty from the other species of the group, but usually similar to those of *ortus* (fig. 30). *Spermatheca* : As for *superstitiosus* (fig. 15).

Colour of dorsal surface : Head reddish-yellow. *Prothorax* with collar whitish or yellowish, anterior fold and lateral margins red, disc and posterior margin yellow, sometimes with a trace of a posterior black fascia. *Corium* yellow with corial fascia present or absent—all gradations are shown from a completely immaculate form (var. *immaculatus* Schmidt) to one with the fascia present as a narrow black line ; a common form bears a small round spot on each corium. *Membrane* variable, rather light in immaculate forms, dark in banded forms.

Colour of ventral surface : In general as in *superstitiosus* (fig. 1), but white usually tinged with yellow, and resembles *nigrofasciatus* in reduction of red on second abdominal segment to a narrow basal infusion. Metathoracic scent gland spout dark but not black.

Legs : Red, tarsi and apex of tibiae usually dark.

Length 10–16.5 mm., *breadth across wings* 3.5–5.5 mm.

A medium sized species from Madagascar and Mascarene Is., allied to *D. nigrofasciatus*.

I have not seen the type.

Distribution of specimens seen : MADAGASCAR : Mt. France, 1 ♂ (*R. V. de Salvaza*) ; Fian, 1 ♀. MAURITIUS : 4 ♂, 3 ♀ (*J. E. M. Brown*) ; 2 ♂, 4 ♀. RODRIGUEZ : 1 ♂, 1 ♀, viii–xi.1938 (*Snell and Thomassett*) ; 2 ♂, 2 ♀ (*Gulliver*).

Type locality : Madagascar.

Dysdercus ortus Distant, 1909.

ortus Distant, 1909a : 36 (*Dysdercus*). Distant, 1913 : 158 (*Dysdercus*). Hussey, 1929 : 98 (*Dysdercus*).

Antennae : First segment hardly longer than second. *Rostrum* : Long, reaching to third and often to fourth abdominal segment ; third segment rather longer than fourth. *Anterior femora* : As in *nigrofasciatus* with distinct small spines in addition to the sub-apical group. *Male genitalia* : Ninth segment as in *nigrofasciatus* (fig. 21). Parameres of

nigrofasciatus type, apex flat, lower tooth more rounded (fig. 30). *Spermatheca*: As for *superstitiosus* (fig. 15).

Colour of dorsal surface: Head yellowish-red, usually darkened posteriorly. *Prothorax* with whitish or yellowish collar, fold and lateral margins red, disc yellowish, posterior black fascia suffusing most of disc with black or dark brown. *Corium* yellow, fascia in form of two large irregular black spots (sometimes a little reduced in size). *Membrane* dark.

Colour of ventral surface: Pattern as in *superstitiosus* (fig. 1), but white replaced by pale yellow and red very dark or suffused with black on meso- and metathorax and some or all of the abdominal segments, much as in *fasciatus* (fig. 2). Metathoracic scent gland spout dark or occasionally black.

Legs: Very dark brown or black except for coxae and trochanters, which are red.

Length 11.5–15.5 mm., *breadth across wings* 3.5–5.0 mm.

A smallish species from Seychelles with an obvious dorsal pattern and dark legs, allied to *D. nigrofasciatus*.

Type in the collection of the British Museum—a female from Praslin, Seychelles, collected by J. S. Gardiner, v-xii.1905.

Distribution of specimens seen: SEYCHELLES: Praslin, v-xii. 1905, 2♂, 1♀ (J. S. Gardiner); Cousin Is., 1♂, 2♀, v-xii.1905 (J. S. Gardiner); Mahe, 1♂, 3♀, 1908–9; no details, 4♀, and 1♂, 3♀ (Wright).

Dysdercus fasciatus Signoret, 1861.

fasciatus Signoret. 1861: 954 (*Dysdercus*). Stål, 1866: 14 and 1870: 118 (*Dysdercus*). Gerstaecker, 1873: 415 (*Dysdercus*). Reuter, 1887: 93 (*Dysdercus*). Gerstaecker, 1892: 50 (*Dysdercus*). Schouteden, 1910: 153 and 1912: 304 and 305 (*Dysdercus*). Distant, 1913: 158 (*Dysdercus*). Courteaux, 1922: 286 (*Dysdercus*). Hussey, 1929: 89 (*Dysdercus*). Blöte, 1931: 121 (*Dysdercus*). Schmidt, 1932: 276 (*Dysdercus*).

scrupulosus Stål, 1861: 199 (*Dysdercus*).

Antennae: First segment hardly longer than second. *Rostrum*: Long, reaching apex of third or centre of fourth abdominal segment; third segment often longer than fourth. *Anterior femora*: In addition to the usual subapical group, there are strong spines along their length, though somewhat reduced in small specimens. *Head* elongate (fig. 2), nearly as long as the prothorax, appears somewhat swollen, quite obviously different from the head of any other African species. *Male genitalia*: Ninth segment (fig. 22) with a dorsal conical process bearing two small black teeth before the apex. *Parameres* (fig. 31) with double hooked apex characteristic of this group, but larger and apex much broader than in any other species. *Spermatheca*: As for *superstitiosus* (fig. 15).

Colour of dorsal surface: Head red, usually slightly darkened posteriorly. *Prothorax* with narrow white collar often margined with black posteriorly; fold and lateral margins red; disc yellowish-red, with posteriorly a broad black fascia in the shape of a narrow ellipse, more or less encroaching on to the disc, posterior margin itself very narrowly pale. *Scutellum* red. *Corium* yellowish-red, often tinged with deep red around the margins; corial fascia in the form of a pair of broad black spots touching both margins and often parallel sided. *Membrane* dark.

Colour of ventral surface: Deep red and white with, in the paler forms, a black anterior border to meso- and metathorax and abdominal segments 1–6. In the darker forms, which appear to be more common, the black spreads until it suffuses much of the two thoracic segments and abdominal segments 1–4 (fig. 2), the final appearance being of a broad black stripe with white cross bands. Reduction of white on the prothorax by red encroaching on to the episternum constant, and the presence of a straight dividing line between red and white, is a good specific character; absence of white on first abdominal segment constant; absence of white on fifth segment usual but not constant. Metathoracic scent gland spout reddish even in the darkest forms.

Legs: Coxae and trochanters red; femora, tibiae and tarsi varying from dark red to black.

Length 10.5–19.5 mm., *breadth across wings* 3.5–6.5 mm.

A large species easily distinguishable by its big head, and large corial and thoracic fasciae.

Colour Variation.

Two specimens from the Blue Nile show the red entirely replaced by yellow even on the legs, which are yellowish-brown; it is possible that they are teneral specimens. Specimens from Aldabra, Cosmoledo and Astove Is. are lighter and more yellowish than those from the mainland; usually the prothoracic fascia is lacking, but all stages are shown in its suppression; in some specimens the femora are clear red and the ventral abdominal black markings practically lacking.

I have not seen the type.

Distribution of the specimens seen: ANGLO-EGYPTIAN SUDAN: Sennar, 3 ♂, 6 ♀, xi.1910 (*S. S. Flower*); Nuba Mts., Kadugli, 1 ♂, 1 ♀ (*F. Moysey*); Blue Nile, 1 ♂, 1 ♀ (*E. S. Crespin*). UGANDA: Kampala, 2 ♂, vii.1911 (*S. A. N.*); Mpumu, 1 ♂, 3 ♀, vii.1911 (*S. A. N.*); Entebbe, 3 ♂, vii.1911 (*S. A. N.*); and 4 ♂, 9 ♀, viii–xii.1911 (*C. C. Gowdey*); Ankole, 1 ♀, x.1911 (*S. A. N.*); Koki Country, 6 ♂, 2 ♀, x.1911 (*S. A. N.*); Entebbe, 9 ♂, 13 ♀, ii.1912 (*C. A. Wiggins*); Uruma, 1 ♂ (*U. Robertson*). KENYA: Voi, 2 ♂, 2 ♀, ii.1911 (*S. A. N.*); Kibwezi, 1 ♂, iv.1911 (*S. A. N.*); Mesongaleni, 5 ♂, 5 ♀, iv.1911 (*S. A. N.*); Mombasa, 1 ♂, 2 ♀, ii.1912 (*S. A. N.*); Witu, 1 ♀, ii.1912 (*S. A. N.*); Uchweni Forest, 2 ♂, 1 ♀, iii.1912 (*S. A. N.*); Nairobi, 1 ♂, vi.1912 (*A. D. Milne*); Tendaguru, 3 ♂, 2 ♀, xii.1924 (*W. E. Cutler*); Mpapwa, 2 ♂, 2 ♀ (*Baxter*); Ngatana, 4 ♂, 3 ♀ (*Gregory*). TANGANYIKA: Ruaha R., 1 ♀, xii.1910 (*S. A. N.*); L. Manyara, 1 ♀, 1935 (*B. Cooper*); Uluguru, 1 ♂, 1 ♀ (*A. G. Wilkins*); ZANZIBAR: 1 ♀ (*W. M. Aders*). NYASALAND: Shores of L. Nyasa, 7 ♂, 10 ♀, iii.1910 (*S. A. N.*); Zomba, 1 ♂, ii.1910 (*S. A. N.*); and 5 ♂, 8 ♀ (*H. S. Stannus*); Chiromo, 1 ♀, iv.1910 (*S. A. N.*); Ruo V., 1 ♀, iv.1910 (*S. A. N.*); Mombera, 2 ♀, vi.1910 (*S. A. N.*); Rukuru R., 4 ♂, 9 ♀, vi.1910 (*S. A. N.*); Karonga, 1 ♂, 1 ♀, vii.1910 (*S. A. N.*); Mlanje, 1 ♂, 1 ♀, vii.1913 (*S. A. N.*); Shire V., 1 ♂, viii.1913 (*S. A. N.*); Domira Bay, 1 ♀, ii.1915 (*W. A. Lamborn*); L. Likoma, 1 ♂, 2 ♀ (*de Jersey*); Ft. Johnston, 1 ♀ (*P. Rendall*); Kotokota, 1 ♂, 6 ♀ (*J. E. S. Old*); no details, 1 ♂, 1 ♀. N. RHODESIA: Algoa, 2 ♀, v.1910; N'Changa, 1 ♂, 1 ♀ (*C. T. Macnamara*). S. RHODESIA: Salisbury, 6 ♂, 3 ♀, 1897 and 2 ♂, 2 ♀, xi.1903 (*G. A. K. Marshall*); also numerous specimens in alcohol (*B. L. Mitchell*). PORTUGUESE EAST AFRICA: Kola R., 1 ♀, iv.1913 (*S. A. N.*); Caia, Zambesi R., 2 ♂, 2 ♀ (*H. Swale*). NATAL: Zululand, Nagana Reserve, 1 ♂, 2 ♀, 1922 (*H. H. Curson*). ANGOLA: 1 ♀. BELGIAN CONGO: Kambove-Katanga, 1 ♀, vi.1907 (*S. A. N.*); no details, 1 ♂, 2 ♀. NIGERIA: Ibadan, 5 ♀, iii.1923 (*A. W. J. Pomeroy*); S. Nigeria, 1 ♂ (*S. A. Jones*). SIERRA LEONE: 1 ♂. GAMBIA: Bathurst, 9 ♂, 9 ♀, ii.1911 (*J. J. Simpson*); no details, 2 ♂, 3 ♀. MADAGASCAR: 1 ♀. ALDABRA I.: 1 ♂, 5 ♀ (*P. R. Dupont*); 1 ♂, 1 ♀ (*J. C. F. Fryer*). COSMOLEDO Is.: 2 ♂, 1 ♀ (*P. R. Dupont*). ASTOVE I.: 1 ♀ (*P. R. Dupont*).

Type locality, "Madagascar et côtes de Zanzibar."

Dysdercus cardinalis Gerstaecker, 1873.

cardinalis Gerstaecker, 1873 : 416 (*Dysdercus*). Distant, 1902b : 543 (*Dysdercus*). Schouteden, 1910 : 153 and 1912 : 304 and 305 (*Dysdercus*). Bergroth, 1920 : 4 (*Dysdercus*). Hussey, 1929 : 86 (*Dysdercus*). Blöte, 1931 : 118 (*Dysdercus*). Schmidt, 1932 : 277 (*Dysdercus*).

Antennae : First segment clearly longer than second, but not as long as two and three together. *Rostrum* : Normal, reaching second abdominal segment. *Anterior femora* : Small distinct spines present along the length ventrally in addition to the subapical group. *Male genitalia* : Ninth segment rounded apically, seen from above with three folds at apex (fig. 23). Parameres very typical (fig. 32), both apical teeth at same level. *Spermatheca* : As for *superstitiosus* (fig. 15).

Colour of dorsal surface : Head red. *Prothorax* with collar white, fold and lateral margins red, disc yellowish-grey and posterior margin concolorous with no indication of a black line. *Scutellum* reddish-yellow. *Corium* yellowish-grey, fascia usually broad and black, normally not reaching outer margin but may do so in occasional specimens. *Membrane* dark.

Colour of ventral surface : General pattern of red and ivory-white very characteristic (fig. 3). First and second abdominal segments almost entirely white, third and fourth with large triangular red spots, fifth with variable white posterior margin, sixth with usual crescent of white. Black entirely lacking on the ventral surface. Metathoracic scent gland spout red tinged with white.

Legs : Entirely red, usually clear red but sometimes slightly dusky.

Length 12.5–19 mm., *breadth across wings* 4.2–6 mm.

A fairly large species easily distinguishable by the broad corial fascia, absence of prothoracic black line, striking ventral abdominal pattern and red legs.

I have not seen the type.

Distribution of specimens seen : **ABYSSINIA** : Shoa, Ambucarra, 4 ♂, 1 ♀, viii.1879 (*Antinori*). **ADEN** : 1 ♀ (*J. J. Walker*) ; 1 ♀. **KENYA** : Samburu, 1 ♀, xi.1896 (*C. S. Betton*) ; Maungu, 1 ♂, iii.1897 (*C. S. Betton*) ; Mito Andei, 1 ♀, ii.1911 (*S. A. N.*) ; Naivasha, 1 ♀, ii.1911 (*S. A. N.*) ; Tsavo R., 1 ♀, ii.1911 (*S. A. N.*) ; Kibwezi, 1 ♀, iv.1911 (*S. A. N.*) ; Makindu, 1 ♀, iv.1911 (*S. A. N.*) ; Masongaleni, 1 ♀, iv.1911 (*S. A. N.*) ; Yala R., 1 ♀, v.1911 (*S. A. N.*) ; Mkunumbi, 1 ♂, 2 ♀, ii.1912 (*S. A. N.*) ; Tiwa R., Ukamba, 1 ♂, 1 ♀, i.1912 (*S. W. J. Scholefield*) ; Mombasa, 3 ♂, 4 ♀, ii.1912 (*S. A. N.*) ; Magogoni Swamp, 1 ♀, ii.1912 (*S. A. N.*) ; Voi, 3 ♀, ii.1912 (*S. A. N.*) ; Kipini, 1 ♂, iii.1912 (*S. A. N.*) ; L. Mpeketoni, 8 ♂, 7 ♀, iii.1912 (*S. A. N.*) ; Magadi, 3 ♂, 5 ♀, iv.1912 (*F. G. Hamilton*) ; Nairobi, 8 ♂, 10 ♀, vi.1912 (*A. D. Milne*) ; Shimba, 2 ♂, 5 ♀, vii.1912 (*A. D. Milne*) ; Nairobi, 1 ♂, 3 ♀, ix.1912 (*A. D. Milne*) ; Mogor R., 1 ♀, v.1913 (*A. O. Luckman*) ; Nairobi, 1 ♂, 1 ♀, vii.1919 (*A. Loveridge*) ; Chyulu Hills, 1 ♂, 2 ♀, vii.1938 (*Coryndon Museum, Nairobi*) ; Kitui, 1 ♂ (*A. W. J. Scholefield*) ; Njoro, 1 ♂, 1 ♀ (*A. J. Cholmley*) ; Watita Hill, 2 ♂, 3 ♀ (*C. Montague-Smyth*). **TANGANYIKA** : Dar-es-Salaam, 1 ♂, vi.1899 (*C. V. Legros*), and 1 ♀, v.1918 (*A. W. J. Pomeroy*) ; Noisinak Bridge, 1 ♂, 1 ♀, v.1916 (*W. A. Lamborn*) ; Kongwa, 1 ♂, 3 ♀, iv.1917 (*A. Loveridge*) ; Mpapwa, 1 ♀ ; no details, 2 ♂ (*A. Loveridge*). **ZANZIBAR** : 1 ♂, 1 ♀, ii.1925 (*H. J. Snell*).

Type locality : Zanzibar.

Dysdercus intermedius Distant, 1902.

intermedius Distant, 1902b : 543 (*Dysdercus*). Schouteden, 1912 : 304 and 305 (*Dysdercus*). Hussey, 1929 : 92 (*Dysdercus*).

Antennae : First segment scarcely longer than second. *Rostrum* : Slightly longer than usual, reaches at least to apex of second abdominal segment, usually to middle of third. *Anterior femora* : In addition to the normal subapical group, there are distinct spines along the length ventrally. *Male genitalia* : Ninth segment conical as in other species of this group, apex with indication of two lobes or slightly indented (fig. 24). Parameres (fig. 34) quite characteristic, apical hooks somewhat cap-like, projection on stem rather small. *Spermatheca* : Duct very long, gland recurved (fig. 16).

Colour of dorsal surface : Head red or orange, darkened behind the eyes. *Prothorax* with white collar edged posteriorly with black and a tendency for the white to be carried posteriorly along the lateral margins; fold and lateral margins red or orange; disc and posterior margin grey or yellowish-grey, posterior margin sometimes whitish, never dark or black. *Scutellum* red or orange. *Corium* disc yellowish-grey, margins broadly yellowish; black corial fascia present, usually in the form of a narrow black line reaching both margins, but may be much reduced. *Membrane* dark.

Colour of ventral surface : Red or orange red and white as in fig. 4; abdominal segments 2-6 black basally and meso- and metathorax black anteriorly. This colour pattern is very constant and the variation shown by other species is not found here. Metathoracic scent gland spout reddish.

Legs : Coxae, trochanters and femora red, tibiae and tarsi dark or black.

Length 14.5-22.5 mm., *breadth across wings* 4.8-7.5 mm.

A large species easily distinguishable by the narrow corial fascia. absence of black thoracic fascia, pattern of venter and conical ninth segment of male.

Type in the collection of the British Museum—a female from Tanganyika.

Distribution of specimens seen : NYASALAND : Zomba, 1 ♂, ii-iii.1896 (*A. Whyte*), 2 ♂, 8 ♀ (*H. S. Stannus*); S.E. and S.W. shores of L. Nyasa, 2 ♂, 5 ♀, iii.1910 (*S. A. N.*); Mlanje Boma, 4 ♂, 2 ♀, iv.1910 (*S. A. N.*); Ruvo V., 7 ♂, 6 ♀, iv.1910 (*S. A. N.*); Lower Shire V., 3 ♂, iv.1910 (*S. A. N.*); Dedza, 1 ♀, v.1910 (*S. A. N.*); Chiromo, 1 ♀, v.1910 (*J. E. S. Old*); S. Rukuru V., 1 ♀, vi.1910 (*S. A. N.*); Blantyre, 8 ♂, 5 ♀, vi-viii.1910 (*J. E. S. Old*); Milengeni, 1 ♀, i.1911 (*J. E. S. Old*); Mlanje, 6 ♂, 3 ♀, ii.1913 (*S. A. N.*); Pt. Herald, 5 ♂, 4 ♀, 1913 (*J. E. S. Old*); Ft. Johnstone, 2 ♀ (*P. Rendall*); no details, 7 ♂, 10 ♀ (*J. E. S. Old*). N. RHODESIA : Petauke, 3 ♂, ix.1910 (*S. A. N.*). S. RHODESIA : Salisbury, 2 ♂, 1 ♀, 1898, 2 ♂, 3 ♀, i.1906 (*G. A. K. Marshall*), 1 ♂, ii.1921 (*C. E. Godman*); Umtali, 2 ♂, 1 ♀, 1897. PORTUGUESE E. AFRICA : Busi, 2 ♀, xii.1906 (*C. F. M. Swynnerton*) and 1 ♂, 3 ♀ v.1915; Caia, Zambesi R., 4 ♂, 4 ♀, vi.1910 (*H. Swale*); Ruvo V., 1 ♂, iv.1913 (*S. A. N.*); Kola, 1 ♂, 1 ♀, v.1913 (*S. A. N.*); Monapo, 1 ♀, x.1918 (*G. D. H. Carpenter*).

Type locality : Tanganyika.

Dysdercus orientalis Schouteden, 1910.

orientalis Schouteden, 1910 : 154 (*Dysdercus*). Schouteden, 1912 : 304 and 305 (*Dysdercus*). Hussey, 1929 : 98 (*Dysdercus*).

pulchra Schouteden, 1910 : 154. Schouteden, 1912 : 303. Hussey, 1929 : 98. (All as var. of *D. orientalis*).

Antennae : First segment slightly longer than second. *Rostrum* : Normal, reaching to second abdominal segment. *Anterior femora* : No spines along their length, only subapical group present. *Male genitalia* : Ninth segment conical, bifid terminally (fig. 25). Parameres quite characteristic as in fig. 35. *Spermatheca* : As *intermedius* (fig. 16).

Colour of dorsal surface : *Head* red, usually darkened posteriorly. *Pronotum* with collar fairly broadly white, the white creeping back along the lateral margins a short distance; fold and lateral margins black, occasionally with red patches; disc orange or ochraceous yellow and posterior margin concolorous—no posterior black fascia. *Scutellum* wholly yellow-orange in light forms, black in dark forms, with intermediate grades black anteriorly and yellow posteriorly. *Corium* concolorous with disc of prothorax; corial fascia in form of broad or narrow black line always touching inner margin of each wing and sometimes touching outer as well. *Membrane* dark.

Colour of ventral surface : Pattern (but not colour) as in *D. haemorrhoidalis* Signoret (fig. 5), but only red on head, thorax and ninth segment of male; abdominal red usually replaced by a very pale yellow, so that venter appears more or less all one colour—i.e., cream or pale yellow. In dark forms (var. *pulchra* Schouteden) red on thorax and yellow on sometimes all, or at least segments 5 and 6 of abdomen, suffused with black. Metathoracic scent gland spout usually reddish even in the darkest forms.

Legs : Typically, coxae, trochanters of all legs, and femora of first and second pairs of legs, red, posterior femora except basally and all tibiae and tarsi black. In very dark forms all femora completely black.

Length 11–14 mm., *breadth across wings* 3.8–5.5 mm.

A fairly small to medium-sized species with black thoracic callus, no posterior black thoracic fascia and often pale venter.

Variation in Colour.

Schouteden, in his original description, described a variety with black thoracic pleura which he named var. *pulchra*. With a fairly long series of this species at my disposal in the British Museum (over 100 specimens), I was able easily to show that a complete gradation exists from forms in which almost all the red and yellow on the ventral surface and femora is replaced by black, to forms almost completely lacking black ventrally and with red anterior and middle femora. Some of the specimens which I have seen are far darker than in Schouteden's description and there seems little point in selecting arbitrary limits for varieties. I have therefore disregarded this varietal name.

I have not seen the type:

Distribution of specimens seen : KENYA : Aberdare Mts., 2 ♂, 12 ♀, ii.1911 (*S. A. N.*); 1 ♂, 4 ♀ (*T. J. Anderson*) and 3 ♂, 2 ♀, x.1934 (*F. W. Edwards*); Mt. Kenya, 5 ♂, 4 ♀, ii.1911 (*S. A. N.*); Meru, 1 ♀, ii.1911 (*S. A. N.*); Kikuyu Escarpment, 4 ♂, 4 ♀, iii.1911 (*S. A. N.*); Kikuyu Forest, Rogoro, 1 ♂, 1 ♀ (*C. S. Betton*); Mt. Elgon, 2 ♂, 5 ♀, vi.1911 (*S. A. N.*); Nairobi, 3 ♀, vi.1912 (*A. D. Milne*) and 2 ♀, 1914 (*E. Stavey*); Mogorri R., 2 ♂, 2 ♀, v.1913 (*A. O. Luckman*); Narok, Masai Reserve, 19 ♂, 22 ♀, iii.1914 (*A. O. Luckman*); Kabete, 1 ♀, iii.1922 (*H. E. Box*). UGANDA : Mutanda, 1 ♂, iii.1911 (*C. H. Marshall*); Mt. Elgon, 1 ♂, 3 ♀ (*G. W. E. Foster*). TANGANYIKA : 1 ♂, iv.1918 (*A. Loveridge*).

Type locality : Kenya, Kilimanjaro.

Dysdercus pretiosus Distant, 1902.

pretiosus Distant, 1902b : 42 (*Dysdercus*). Distant, 1909b : 79 (*Dysdercus*). Schouteden, 1912 : 304 and 305 (*Dysdercus*). Hussey, 1929 : 100 (*Dysdercus*).

fallax Schouteden, 1910 : 154. Hussey, 1929 : 100. (Both as var. of *D. pretiosus*).

Antennae : Rather long, though exact length variable ; first segment distinctly longer than second. *Rostrum* : Normal, reaches to apex of second abdominal segment. *Anterior femora* : Very strongly spinose and somewhat swollen, spines arising along whole length ventrally, though sometimes not very obvious on basal third, spines longer towards apex. Four specimens examined from Kambove, Katanga (Congo), have greatly reduced spines—in one specimen missing altogether on one side but there are indications of spines on the other femur. Examination of long series from many localities might show a complete gradation to *haemorrhoidalis*. *Male genitalia* : Ninth segment conical, less deeply bifid than in *haemorrhoidalis* and lobes broader and flatter (fig. 26) ; this is a normal but not constant character as occasional specimens are difficult to separate. Parameres as in fig. 36 ; stronger and more curved than in *haemorrhoidalis* though some specimens are difficult to separate (these are not specimens with reduced femoral spines). *Spermatheca* : More variable than in most species ; duct long as in *intermedius*, but accessory gland sometimes nearly straight ; the more recurved *intermedius* type gland commoner in yellow forms.

Colour of dorsal surface : Head black. Prothorax with white collar, rather broader than is usual and slightly extended back along the margins ; fold and lateral margins red, orange, or yellow ; disc dirty white or very light grey, no posterior black fascia. Scutellum black, yellow apically in light forms (var. *fallax* Schouteden). Corium grey or yellowish-grey, often with a yellow suffusion centrally from base to apex ; corial fascia normally very broad indeed, widening as it approaches costal margin which it touches very broadly, giving a characteristic appearance ; in light specimens corial fascia reduced, sometimes to such an extent that it may not even reach either margin. Membrane dark.

Colour of ventral surface : Pattern similar to that of *D. haemorrhoidalis* Signoret (fig. 5), though usually more white on fifth segment. Colours usually red and white, but may be orange or yellow and white ; coloration of fifth and sixth segments never dark and striking. Metathoracic scent gland spout always pale in some degree, sometimes very pale.

Legs : Coxae and trochanters red, remainder of legs usually black, but specimens with femora reddish basally or clear red throughout do occur.

Length 11–15 mm., breadth across wings 4.2–6 mm.

A medium-sized species easily distinguished from all species but *D. haemorrhoidalis* Signoret by black head, pale thorax, and usually very broad corial fascia. Distinguished from *D. haemorrhoidalis* Signoret by spinose anterior femora.

Variation in Colour.

Specimens can be divided roughly into two groups : (a) those resembling the type with broad corial fascia and red prothoracic fold and venter, and (b) those with narrow or much reduced fascia and yellow or orange prothoracic fold and venter. The latter are var. *fallax* of Schouteden. It is not easy to draw a hard-and-fast line between the two forms and so I have omitted the name *fallax*. It is possible that it is seasonal in a similar way to the yellow var. of *D. supersticiosus* (Fabricius). The yellow forms tend to have a more recurved accessory gland to the spermatheca.

The type is in the collection of the British Museum ; it is a female from Ruwenzori collected by Scott Elliot.

Distribution of specimens seen: KENYA: Mt. Kenya, 2 ♂, 2 ♀, ii.1911 (*S. A. N.*); Nandi Escarpment, 1 ♂, v.1911 (*S. A. N.*) Yala R., 2 ♂, v.1911 (*S. A. N.*); Kasout, 1 ♂, 3 ♀, xi.1911 (*S. A. N.*); Narosura, Masai Reserve, 2 ♂, 1 ♀, ii.1914 (*A. O. Luckman*); Karura Forest, 2 ♂, 2 ♀, viii.1919 (*A. Loveridge*); Nairobi, 2 ♀, x.1929 (*G. A. K. Marshall*); Marsabit, 2 ♂ (*S. A. Neave*); Mpapwa, 1 ♀ (*Baxter*). UGANDA: Kagera, 1 ♀, vi.1911 (*C. H. Marshall*); Kampala, 2 ♂, 1 ♀, viii.1911 (*S. A. N.*); W. Ankole, 1 ♀, x.1911 (*S. A. N.*); Mt. Kokanjero, 4 ♂, 1 ♀, viii.1911 (*S. A. N.*); L. George, 2 ♂, 3 ♀, x.1911 (*S. A. N.*); Toro, 14 ♂, 16 ♀, x.1911 (*S. A. N.*); Buamba Forest, 3 ♂, 6 ♀, xi.1911 (*S. A. N.*); Mabira Forest, 3 ♂, 8 ♀, vii.1913 (*C. C. Gowdey*); Katonga R., 1 ♂, 1 ♀, xi.1913 (*C. C. Gowdey*); Entebbe, 6 ♂, 4 ♀, viii.1918 (*C. A. Wiggins*); Namwamba V., 6 ♂, 2 ♀, xii.1934 (*F. W. Edwards*); Ruwenzori, 3 ♂, 3 ♀ (*Scott Elliot*). TANGANYIKA: Kongwa, 1 ♂, 2 ♀, iv.1917 (*A. Loveridge*); no details, 3 ♂, 2 ♀ (*A. Loveridge*). BELGIAN CONGO: Kambove Katanga, 3 ♂, 1 ♀, iii.1907 (*S. A. N.*).

· *Dysdercus haemorrhoidalis* Signoret, 1858.

haemorrhoidalis Signoret, 1858 : 308 (*Dysdercus*).

haemorrhoidalis Stål, 1866 : 16 emend. (*Dysdercus*). Stål, 1870 : 119 (*Dysdercus*). Schouteden, 1912 : 305 (*Dysdercus*). Hussey, 1929 : 91 (*Dysdercus*). Blöte, 1931 : 122 (*Dysdercus*).

✓ *ugandanus* Schouteden, 1912 : 304 and 305 (*Dysdercus*). Hussey, 1929 : 105 (*Dysdercus*). syn. nov.

Antennae and *rostrum* as in *pretiosus*. *Anterior femora* : With subapical group of spines, two or three in number, only; femora not swollen. *Male genitalia* : Ninth segment conical, apex deeply bifid as in *orientalis* (fig. 25), each half more or less rounded, seldom flattened as *pretiosus*. *Parameres* as in fig. 37; less robust and curved than *pretiosus*. *Spermatheca* : As *intermedius* (fig. 16).

Colour of dorsal surface : Head varying from clear red (*haemorrhoidalis*) to black (*ugandanus*). *Prothorax* with white collar tending to spread back along the margins; fold and lateral margins orange or red; disc grey or yellowish-grey; no posterior black fascia. *Scutellum* orange or red. *Corium* grey with a yellow insuffusion centrally from base to apex, fascia broad and each half reaches both margins of wing—the costal one rather broadly. *Membrane* dark.

Colour of ventral surface : Typically red and white with pattern as in fig. 5; fifth and sixth abdominal segments dark and often suffused with black—a very obvious and good specific character; length of narrow white band on fifth segment variable. Red on segments 1–4 may be replaced by yellow or orange, but segments 5–6 always red. *Meta-thoracic* scent gland spout reddish.

Legs : Reddish or suffused with black, except for coxae and trochanters which are always red.

Length 11–15.5 mm., breadth across wings 4–5.5 mm.

A medium sized species resembling *D. pretiosus* Distant, but separable by the absence of spines on the anterior femora and the colour of the fifth and sixth abdominal segments.

Geographical Variation.

The specimens of this species in the British Museum are divisible into two groups: those from West Africa and those from East Africa. The Western specimens have red heads and legs both with a varying amount of black suffusion; those from the East have black heads and

legs relieved by patches of red. The two groups together form a series, with the Eastern specimens most closely approaching *D. pretiosus* Distant in appearance and pattern (they are of course the *D. ugandanus* of Schouteden); the Western specimens are less strikingly different from the other Ethiopian species in appearance, the corial fascia being on the whole more narrow than in *D. pretiosus* Distant.

I have not seen the type.

Distribution of specimens seen: W. AFRICA—NIGERIA: Ibadan, 2 ♂, 9 ♀, iii.1923 (*A. W. J. Pomeroy*) and 1 ♂, 2 ♀, i.1927 (*F. D. Golding*). CAMEROONS: Mbussa, 1 ♀, iv.1914. E. AFRICA—KENYA: N. Kavirondo, 3 ♂, 1 ♀, v.1911 (*S. A. N.*); S. Kavirondo, 1 ♂, v.1911 (*S. A. N.*). UGANDA: Entebbe (coll. *C. C. Gowdey* and *C. A. Wiggins*) 2 ♀, viii.1911, 1 ♂, 4 ♀, v.1912, 1 ♀, ix.1912, 1 ♀, x.1912, 1 ♂, 1 ♀, xi.1912, 6 ♂, xii.1912, 2 ♀ i.1913, 1 ♂, iv.1913, 1 ♂, 2 ♀, v.1913; Masindi, 1 ♂, xii.1911 (*S. A. N.*); Katonga R., 1 ♂, xi.1913 (*C. C. Gowdey*); Kampala, 1 ♀, xii.1915 (*C. C. Gowdey*).

Type locality: Gaboon.

Dysdercus koenigii (Fabricius, 1775).

koenigii Fabricius, 1775: 720 (*Cimex*). Goeze, 1778: 257 (*Cimex*). Fabricius, 1781: 364 and 1787: 299 (*Cimex*). Gmelin, 1788: 2172 (*Cimex*). Fabricius, 1794: 155 and 1803: 222 (*Lygaeus*). Wolff, 1800: 28 (*Lygaeus*). Laporte, 1833: 37 (*Astemma*). Hahn, 1834: 12 (*Pyrrhocoris*). Spinola, 1837: 177 (*Lygaeus*). Amyot and Serville, 1843: 272 (*Dysdercus*). Herrich-Schäffer, 1853: 177 (*Dysdercus*). Stål, 1868: 84 (*Dysdercus*). Bergroth, 1914: 855 (*Dysdercus*). Hussey, 1929: 92 (*Dysdercus*). Schmidt, 1932: 260 in part (*Dysdercus*).

superstitiosus Stål, 1866: 15 in part (*Dysdercus*).

cingulatus Stål, 1870a: 119 in part (*Dysdercus*). Distant, 1879: 127 (*Dysdercus*)? Distant, 1888: 484 in part (*Dysdercus*). Kirby, 1891: 104 in part (*Dysdercus*). Kirkaldy, 1900: 295 and 1901: 301 (*Dysdercus*). Breddin, 1901a: 84 in part (*Dysdercus*). Kirkaldy and Edwards, 1902: 171 in part. (*Astemma*) Distant, 1904: 118 in part and 1910: 100 in part (*Dysdercus*).

micropygus Breddin, 1909: 299 (*Dysdercus*). Bergroth, 1913: 173 (*Dysdercus*).

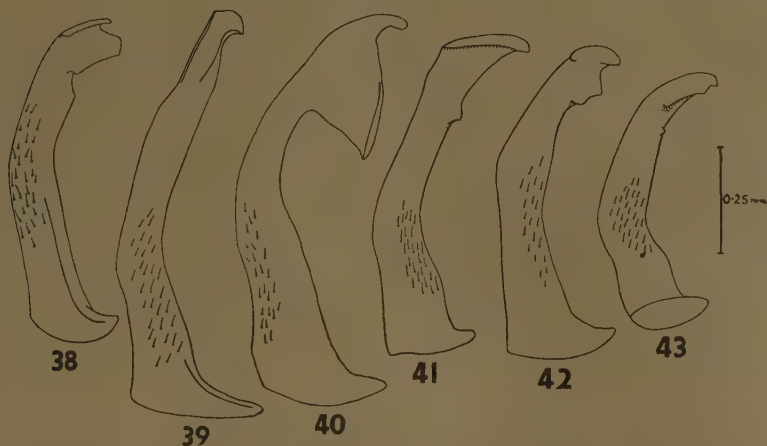
Antennae: First segment longer than second but not as long as second and third together. *Rostrum*: Normal, reaches to second or base of third abdominal segment. *Anterior femora*: Subapical group of spines only present. *Prothorax*: As in *cingulatus* (fig. 7), narrower posteriorly than *olivaceus*. *Male genitalia*: Ninth segment rather rounded ventrally with a medium transverse impression; upturned apex somewhat abrupt and bilobed. Parameres (fig. 38) somewhat variable, of the normal two crested form typical of this group. Vertical processes (fig. 44) rather transparent. Second conjunctiva appendages simple (fig. 13). *Spermatheca*: Duct very short (fig. 17), gland more coiled than in *cingulatus*.

Colour of dorsal surface: Head red. *Prothorax* with white crescentic collar, anterior fold, anterior angles and lateral margins red, usually with no trace of black, disc and posterior margin yellowish or reddish concolorous with corium. *Scutellum* red or black or intermediate. *Corium* uniformly yellowish or reddish with centrally placed oval black spot variable in size, but never touching either margin. *Membrane* dark.

Colour of ventral surface: Normally clear red and white with a pattern similar to that of *superstitiosus* (fig. 1), but abdominal fasciae (on segments 1–6) rather narrow, usually less than half the width of the segment. In very dark specimens abdominal incisures and margins of meso- and metathorax may be narrowly black.

Legs Coxae, trochanters and femora nearly always clear red throughout, tibiae and tarsi dark or tibiae reddish basally; in very dark specimens femora may be dark apically

Length 11–15.5 mm., *breadth across wings* 2.5–5.0 mm.



FIGS. 38-43.—Lateral view of right parameres of Oriental and Australasian species. (38) *D. koenigii* (Fabricius); (39) *D. cingulatus* (Fabricius); (40) *D. sidae* Montrouzier; (41) *D. longiceps* Breddin; (42) *D. mesiostigma* Distant; (43) *D. decussatus* Boisduval.

Readily distinguished from all species except *cingulatus* by its fairly uniform dorsal colouring, normal ventral pattern, centrally placed black corial spots and narrower thorax; distinguished from *cingulatus* by male genitalia, spermatheca, usually clear red femora and absence of black on prothoracic fold, and its Indian distribution.

I have not seen the type.

Distribution of specimens seen: CEYLON: Galle, 2 ♂, 3 ♀ and Tala, 2 ♀, ii.1909 (*T. B. Fletcher*); Trincomalee, 3 ♀; no details, 2 ♀ (*Lewis*) and 1 ♂, 1 ♀. S. INDIA: 2 ♂, 5 ♀ (*Campbell*). MYSORE: Bangalore, 2 ♀ (*Cameron*). BOMBAY: 1 ♀ (*Wren*); 3 ♀ (*Dixon*). RAJPUTANA: Surajgarh, 1 ♀. PUNJAB: Multan, 5 ♂, 4 ♀, v.1923 (*J. E. M. Boyd*). UNITED PROVINCES: Meerut, 2 ♂ (*Atkinson*); Kumaun, 1 ♂; Agra, 1 ♂, 1 ♀, xii.1927 (*T. D. A. Cockerell*); Dehra Dun, 1 ♀. BIHAR: 1 ♀, vii.1915. BENGAL: Darjeeling, 1 ♀ (*G. Rogers*); Calcutta, 3 ♂, 2 ♀ (*Atkinson*). BURMA: Shwegyin, N. Pegu, 1 ♂ (*Atkinson*) (correct locality?).

Type locality, Madras: Tranquebar.

Mehta (1930) deals with the biology of this species under the name of *D. cingulatus*.

Dysdercus solenis (Herrich-Schäffer, 1844).

solenis Herrich-Schäffer, 1844: 18 (*Pyrrhocoris*). Herrich-Schäffer, 1853: 177 (*Dysdercus*). Carpenter, 1891: 141 (as var. of *D. cingulatus*). Bergroth, 1913: 172 (as var. of *D. cingulatus*). Bergroth, 1914: 355 (*Dysdercus*). Hussey, 1929: 103 (*Dysdercus*). Blöte, 1931: 132 (*Dysdercus*).

cingulatus Stål, 1870: 119 in part (*Dysdercus*).

ellanorae Banks, 1909: 578 (*Dysdercus*).

solenis Taeuber, 1927: 192 and 195 (*Dysdercus*).

Antennae : Normal, first segment longer than second but not subequal to two and three together. *Rostrum* : Normal, reaches second abdominal segment. *Anterior femora* : Subapical spines present only. *Eyes* : Rather larger than is usual, width of each eye equal to half width of vertex between eyes. *Male genitalia* : Ninth segment with broadly conical upturned apex. Parameres of *koenigii* type (fig. 38). Vertical processes fairly broad but pointed at the apex and divergent (fig. 45). Second conjunctiva appendage simple.

Colour of dorsal surface : In what is apparently the normal form, head, pronotum, except the collar, and scutellum red ; pronotal collar white ; corium grey with costal margin broadly and strikingly red ; corial black spots large and oval, not touching either margin ; membrane dark. In the specimen from Borneo all the red on upper, lower surfaces and legs is replaced by yellow, which though less striking than the red is still clearly different from the grey of the corial disc ; black spots of this specimen smaller and round.

Colour of ventral surface : Red and white or yellow and white, black entirely absent ; thoracic markings as in *superstitiosus* (fig. 1) ; abdominal segments 1-6 with white fasciae, broader laterally and contracted ventrally much as in *superstitiosus*.

Legs : Coxae, trochanters and femora red (yellow in the Borneo specimen) ; tibiae and tarsi dark which may encroach on to apex of femora.

Length 12.5-18 mm., *breadth across wings* 4-5.5 mm.

A medium sized to large species distinguished by the red or yellow margins to the corium and the larger eyes.

I have not seen the type.

Distribution of specimens seen : PHILIPPINE IS. : 1 ♀ (*E. M. Ledyard*). BORNEO : 1 ♂ (*Bohac*). CELEBES : 1 ♂ (*Wallace*).

Type locality : Philippine Is.

Dysdercus evanescens Distant, 1902.

evanescens Distant, 1902a : 43 (*Dysdercus*). Kirkaldy and Edwards, 1902 : 172 (*Astemma*).

Distant, 1904 : 120 (*Dysdercus*). Bergroth, 1913 : 173 (*Dysdercus*). Hussey, 1929 : 89 (*Dysdercus*). Blöte, 1931 : 121 (*Dysdercus*).

Antennae : Normal, second segment shorter than first. *Rostrum* : Normal, reaches second abdominal segment. *Sculpture* : Punctuation rather stronger than is usual, especially on white portions of thoracic pleura. *Anterior femora* : Lightly spined along apical half, in addition to subapical group of spines. *Male genitalia* : Ninth segment with upturned apex somewhat abrupt and bilobed. Parameres of usual *koenigii* type (fig. 38). Vertical processes broad and apically rounded (fig. 48), slightly divergent. Second conjunctiva appendages simple. *Spermatheca* : As *koenigii* (fig. 17).

Colour of dorsal surface : Head, disc and posterior margin of prothorax, scutellum, clavus and corium concolorous, varying from light greyish ochraceous to deep red, with head occasionally rather more orange and in light forms margins of corium sometimes reddish. Anterior pronotal collar either white (lighter forms) or concolorous (darker forms) ; fold and lateral margins orange or red (lighter forms) or concolorous (darker forms). Small black elongate oval spot on each corium placed more or less centrally, sometimes practically absent, always very small for size of insect. Membrane pale.

Colour of ventral surface : Light forms show red and white fasciation of thorax and segments 1-6 of abdomen reminiscent of *superstitiosus* (fig. 1) with anterior border of segments 2-6 black. In darker forms this fasciation is more or less obscured by suffusion of the white by pink or red on both thorax and abdomen. Abdominal segments 2-6 are always narrowly black anteriorly, sometimes laterally only, but often stretching right across venter.

Legs : Entirely red in all specimens seen, with sometimes the tarsi slightly infuscated.

Length 15-19.5 mm., *breadth across wings* 5-6.5 mm.

A fairly large species easily recognised by the pale membrane and small transverse corial spots.

Type, a female from Mungphu, Sikkim, India, in the collection of the British Museum.

Distribution of specimens seen : BOMBAY PRESIDENCY : N. Konkan, 1 ♂, 3 ♀ (*Dixon*). BENGAL : Kurseong, 1 ♀; Darjeeling, 1 ♂, 6 ♀, vi.1914 (*H. Stevens*). SIKKIM : Gantok, 1 ♂, 3 ♀, iv.1924 (*R. W. G. Hingston*); Tankola, 2 ♀, ii.1920 (*H. Stevens*); Rungbong V., 1 ♀ (*H. Stevens*); Mungphu, 3 ♀ (*Atkinson*); no details, 1 ♂, 5 ♀ (*Atkinson*). ASSAM : Khasia, 2 ♀; Naga Hills, 1 ♀; no details, 2 ♂, 1 ♀ (*W. F. Badgley*). N. W. PROVINCES : Kumaun, 2 ♂, 1 ♀; Almora District, 1 ♀ (*S. R. Archer*). BURMA : Rangoon, 1 ♀. FRENCH INDO-CHINA : Tongking, Chapa, 2 ♂, 1 ♀, vi.1916 (*R. V. de Salvaza*).

Dysdercus olivaceus (Fabricius, 1798).

olivaceus Fabricius, 1798 : 540 (*Lygaeus*). Fabricius, 1803 : 227 (*Lygaeus*). Stål, 1868 : 84 and 1870a : 119 (*Dysdercus*). Distant, 1904 : 119 (*Dysdercus*). Bergroth, 1914 : 355 (*Dysdercus*). Hussey, 1929 : 98 (*Dysdercus*).

cingulatus Distant, 1904 : 119 in part and 1910 : 100 in part (*Dysdercus*).

luteolus Breddin, 1909 : 300 (*Dysdercus*). Bergroth, 1913 : 173 (*Dysdercus*).

Antennae : Normal, first segment longer than second but not as long as two and three together. *Rostrum* : Normal, reaching apex of second abdominal segment. *Anterior femora* : Only subapical group of spines present, no spines along the length. *Prothorax* broader posteriorly (fig. 8) than *cingulatus*. *Male genitalia* : Ninth segment upturned apex, broadly bilobed, externally rounded with a deep transverse impression ventrally. Parameres of *koenigii* type. Vertical processes broad, transparent and shining, bluntly pointed (fig. 46), often bent apically in a forward direction. Second conjunctiva appendages simple. *Spermatheca* : As *koenigii* (fig. 17) but duct rather longer.

Colour of dorsal surface : Head red. *Prothorax* collar white, fold black or occasionally reddish or even completely red, lateral margins pale or reddish, disc and posterior margin pale dull yellow. *Scutellum* black, inclined to reddish if prothoracic fold pale. *Corium* concolorous with disc of prothorax, black corial spots usually circular, centrally placed, variable in size. *Membrane* dark.

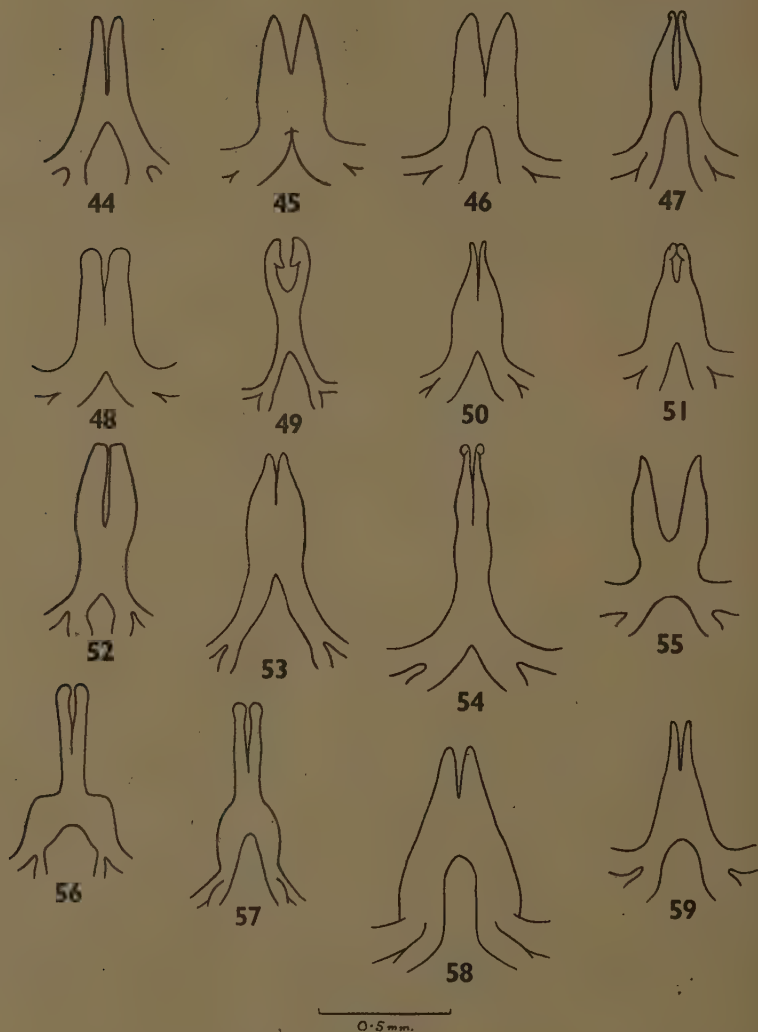
Colour of ventral surface : Reddish inclined to black with white fasciae (fig. 6). *Prothoracic* collar white, posterior prothoracic fascia with more or less straight upper edge; meso- and metathorax with white coxal cavities and epimera as usual. Abdominal segments 1-6 with white fasciae, those on segments 2-3 and sometimes 4-5 forked as shown. This forking is highly variable and may be almost, but never quite, absent, rendering the species difficult to separate from *similis* sp. n. Red colour often replaced laterally and broadly by black between white markings which are narrowed ventrally.

Legs : Usually dark, but femora red in light specimens; coxae, trochanters and base of femora often red.

Length 11.0-15.5 mm., *breadth across wings* 4-5.5 mm.

A pale medium sized species with red head, wide thorax, circular corial spots and forked ventral fasciae; distinguished from *D. similis* sp. n. by the obvious signs of forked ventral fasciae and by the male genitalia.

I have not seen the type.



FIGS. 44-59. Posterior view of vertical processes of ninth segment. (44) *D. koenigii* (Fabricius); (45) *D. solenis* (Herrich-Schäffer); (46) *D. olivaceus* (Fabricius); (47) *D. similis* sp. n.; (48) *D. evanescens* Distant; (49) *D. concinnulus* Walker; (50) *D. poecilus* (Herrich-Schäffer); (51) *D. transversalis* Blöte; (52) *D. festivus* Gerstaecker; (53) *D. cingulatus* (Fabricius); (54) *D. sidae* Montrouzier; (55) *D. longiceps* Breddin; (56) *D. argillaceus* Bergroth; (57) *D. oceanicus* Boisdual; (58) *D. mesiostigma* Distant; (59) *D. decussatus* Boisdual.

Distribution of specimens seen : MYSORE : Nilgiri, 1 ♀ (*Hampson*). MADRAS : Utakamand, 2 ♂ (*Atkinson*); Coimbatore District, 1 ♂, iv.1937; Travancore, 1 ♀ (*G. S. Imray*), 1 ♂, 2 ♀, v.1937; no details, 1 ♂, 1 ♀ (*Campbell*). CEYLON : Peradeniya, 1 ♂, 2 ♀, viii.1900; Badulla, 1 ♀, xii.1908; Kandy, 1 ♂, 1 ♀, ix.1914 (*Whittle*); Colombo, 1 ♀; Punduloya, 1 ♀ (*Atkinson*); no details, 2 ♀ (*Green*), 1 ♂ (*Lewis*), 3 ♀ (*Atkinson*).

Type locality : India.

Dysdercus similis sp. n.

Antennae : Normal, as in *olivaceus*. *Rostrum* : As for *olivaceus*. *Anterior femora* : Sub-apical spines only present. *Prothorax* as for *olivaceus*. *Male genitalia* : Ninth segment with upturned apex broadly conical, never bilobed; ventrally flatter than *olivaceus* and only lightly impressed. Parameres of *koenigii* type. Vertical processes (fig. 47) much narrower, less transparent and closer together than those of *olivaceus*. Second conjunctiva appendages simple. *Spermatheca* : As *koenigii* (fig. 17).

Colour of dorsal surface : As for *olivaceus*.

Colour of ventral surface : Similar to *olivaceus* except that abdominal fasciae never truly bifid, often simple and narrow or may be pointed anteriorly, but point never grows into a true fork.

Legs : Coloured as *olivaceus*.

Length 8–15 mm., *breadth across wings* 2.5–5 mm.

Only to be distinguished with certainty from *D. olivaceus* by structure of male genitalia, but in general may be separated by the simple nature of the abdominal fasciae.

Type, male, S. India, Walayer, Coimbatore District, 19.iv.1937. Allotype, female, same data, both in the British Museum. Paratypes : same data as type, 2 ♀. MADRAS : Yemmiganur, Bellary District, 1 ♀, xii.1913 (*Ponniiah*); Shevaroy, 1 ♀, ix.1914 (*P. S. Cold*); Cumbum, Madura District, 1 ♀, vi.1914 (*S. H. Prater*); Coimbatore, 2 ♀, xi–xii.1914, 1 ♂, v.1930; Naraikkadu, Tinnevely District, 2 ♂, iii.1936; Sethumadai, nr. Pollachi, 3 ♀, iv.1937; Anaimalai, nr. Pollachi, 2 ♀, iv.1937; Top Slip Camp, Nelliampathi Hills, 1 ♂, iv.1937; Coornoor, 1 ♂, 1 ♀; Utakamand, 2 ♀; no details, 3 ♂, 6 ♀ (*Campbell*). CEYLON : Hambantota, 1 ♀, i.1909 (*T. B. Fletcher*); Peradeniya, 1 ♂, viii.1914 (*Rutherford*); no details, 1 ♂ (*Lewis*).

Dysdercus poecilus (Herrich-Schäffer, 1844).

poecilus Herrich-Schäffer, 1844 : 17 (*Pyrrhocoris*). Herrich-Schäffer, 1853 : 177 (*Dysdercus*). Walker, 1872 : 186 (*Dysdercus*). Breddin, 1901a : 85 and 1901e : 145 (*Dysdercus*). Distant, 1902a : 42 and 45 in part (*Dysdercus*). Kirkaldy and Edwards, 1902 : 171 and 172 (*Astemma*). Breddin, 1905a : 129 (*Dysdercus*). Kirkaldy, 1905 : 346 (*Dysdercus*). Banks, 1909 : 578 (*Dysdercus*). Bergroth, 1913 : 173 in part and 1914 : 355 in part (*Dysdercus*). Esaki, 1926 : 158 (*Dysdercus*). Taeuber, 1927 : 193 and 195 (*Dysdercus*). Hussey, 1929 : 99 in part (*Dysdercus*). Blöte, 1931 : 130 (*Dysdercus*). Schmidt, 1932 : 261 (*Dysdercus*).

cingulatus Stål, 1870a : 119 in part (*Dysdercus*).

semifuscus Breddin, 1901a : 85. Taeuber, 1927 : 193. Hussey, 1929 : 100. Blöte, 1931 : 131. (All as var. of *D. poecilus*).

simplex Breddin (*nec* Walker), 1901a : 85 (as var. of *D. poecilus*).

vacillans Hussey, 1929 : 100 (*nom. nov.* for *D. poecilus* var. *simplex* Breddin). Blöte, 1931 : 131 (as var. of *D. poecilus*).

Antennae: Normal, first segment longer than second. *Rostrum*: Normal, reaching to second abdominal segment, or sometimes to base of third. *Anterior femora*: Subapical group of spines present only. *Proportions of head and thorax*: Head rather large (fig. 9), thorax usually with a distinct waist giving a characteristic facies. *Male genitalia*: Ninth segment with upturned tip usually conical and narrow but sometimes reduced in size. Parameres of *koenigii* type. Vertical processes strongly narrowed towards the apices, convergent (fig. 50). Second conjunctiva appendages simple, *Spermatheca*: As *cingulatus* (fig. 18).

Colour of dorsal surface: Head red. *Prothorax* with collar white, extending back along lateral margins often for width of fold; fold black, red or intermediate; disc and posterior margin red or orange. *Scutellum* black, occasionally dusky red in lighter forms. *Corium* concolorous with disc of prothorax; corial spots in normal specimens large, roughly circular, touching or very close to inner margin, clearly much more distant from outer margin; spots may be much reduced or even absent, but never in the form of transverse lines; or corium and clavus may be largely infuscated but costal margin always pale, infuscation present mainly along clavus, claval and apical margins of corium, spots usually visible through darkening. I have seen series collected in one locality showing a complete transition from the immaculate to the darkest form. *Membrane* dark.

Colour of ventral surface: In pale forms red with white fasciae, in dark forms red more or less completely infuscated except along abdominal margin. *Prothorax* with white collar, posterior margin and coxal cavity white, forming a straight diagonal white line. *Meso- and metathorax* margined as usual. First abdominal segment always either immaculate red or dark or only with the slightest trace of white posteriorly, never with a clear white posterior margin as in *concinulus* and other species; segments 2, 3 and 4 bear strong white fasciae, laterally widened to half segment width or more, ventrally contracted to narrow bands; segment 5 with a narrow band and 6 with the usual crescent.

Legs: Coxae and trochanters pale, femora varying from completely black to completely red, tibiae and tarsi usually dark but very occasionally tinged with red.

Length 8.5–13.0 mm., *breadth across wings* 2.5–4.5 mm.

A small species distinguished by the roundish spot touching the inner margin only and in immaculate forms by the absence of a white fascia on the (true) first abdominal segment and the white prothoracic collar reaching back along margins; it is also one of the few species which may be largely infuscated on the dorsal surface.

I have not seen the type. I am omitting Breddin's two varieties *semifuscus* (the form with darkened corium) and *simplex* (*vacillans* Hussey) (the immaculate form), because, as described above, complete series exist connecting both extremes.

Distribution of specimens seen: SIKKIM: 1 ♀ (*Atkinson*). ASSAM: Naga Hills, 1 ♂, 1 ♀; Khasia Hills, 5 ♀ (*Atkinson*); N. Lakhimpur, 1 ♀ (*E. A. W. Hill*); no detail, 1 ♀. BURMA: Bhamo, 1 ♀, vi.1885. SIAM: Biserat, 2 ♀; Neing Sa, 1 ♀; ii.1928 (*A. Mackie*). FRENCH INDO-CHINA: Tatham, 1 ♀, ix.1915; Paklay, 3 ♀, viii.1917; Luang Prabang, 2 ♂, xi.1917; Ban Quang, 1 ♀, iv.1918; Chien Kwang, 3 ♂, 3 ♀, viii.1919; Vientiane, 1 ♂, 1 ♀, x.1919; Chien Kong, 1 ♂, iv.1920; Tonkin, 2 ♂, 1 ♀; Annam, Hue, 1 ♀, ii.1917 (all coll. *R. V. de Salvaza*). CHINA: Hainan, 1 ♂, 5 ♀, vi.1904; Hong Kong, 1 ♀, 1893 (*J. J. Walker*), and 3 ♀. FORMOSA: Suishako, 1 ♂, 1 ♀; no details, 1 ♂. MALAY STATES: Prov. Wellesley, 1 ♀ (*H. N. Ridley*); Perak, 1 ♀ (*Doherty*); Singapore, 1 ♂, vi.1891 (*H. W. Whyte*). SUMATRA: Padang, 1 ♀ (*Ericson*); Medan, 1 ♀ (*J. B. Corporaal*); Fort de Kock, 1 ♂ (*E. Jacobson*); no details, 1 ♂, 4 ♀;

Tello I., 1 ♀, xi.1924. JAVA : Buitenzorg, 1 ♂, 1874 (*G. B. Ferrari*); Tjigomborg, 1 ♀ (*C. W. Andrews*); Batavia, 1 ♀; no details, 1 ♀. BALI : Kintamani, 3 ♂, 1 ♀ (*E. Stresemann*). BORNEO : Sanga Sanga, 1 ♀ (*H. D. Jensen*); N. Borneo, 3 ♀; S.E. Borneo, 1 ♂ (*Doherty*); Sarawak, Mt. Dulit, 6 ♂, 10 ♀, ix.1932 (*Hobby and Moore*); no details, 1 ♀ (*Shelford*); Pulo Laut, 1 ♀ (*Gribodo*). SULU Is. : Jolo, 4 ♀. PHILIPPINE Is. : Mindanao : Zamboanga, 10 ♂, 8 ♀; Camiguin, 1 ♀; Cebu, 3 ♂, 3 ♀; Samar : Pasangan, 1 ♂, ii.1875; Luzon : Manilla, 2 ♂, 11 ♀, 1890; no details, 19 ♂, 14 ♀ (coll. *E. M. Ledyard* and *J. J. Mounsey*).

Type locality : Java.

Dysdercus transversalis Blöte, 1931.

transversalis Blöte, 1931 : 132 (*Dysdercus*).

Antennae, *rostrum*, *anterior femora* and *proportions of head and thorax* as for *poecilus* (above). *Male genitalia* : Ninth segment upturned apex small and conical. Parameres of normal *koenigii* type. Vertical processes (fig. 51) short, rounded, shining and with a distinct "head" not as large as in *concinulus* but quite distinct from *poecilus*. Second conjunctiva appendages simple. *Spermatheca* : As *cingulatus* (fig. 18).

Colour of dorsal surface : Head red. *Prothorax* with collar white extending back as in *poecilus*; fold black or red or intermediate; lateral margins pale; disc and posterior margin reddish or yellowish, concolorous with corium. *Scutellum* black or red. *Corium* concolorous with disc of prothorax, black corial spots narrow, elongate, touching inner but not outer margin, size variable. *Membrane* dark.

Colour of ventral surface : Head red; thorax red and white as in *superstitiosus* (fig. 1). Abdominal segments 1-5 in majority of specimens I have examined, pale usually with dark streak laterally along anterior border; segment 6 mainly dark or black, apical crescent white. In one specimen the dark on segments 1-5 has spread posteriorly, producing a form with fasciated abdomen, white and dark. In other specimens the dark of these fasciae is replaced entirely by red even on segment 6.

Legs : Coxae, trochanters and sometimes base or whole of femora reddish; tibiae, tarsi and remainder or whole of femora dark.

Length 10-15.5 mm., *breadth across wings* 3.5-5.5 mm.

A small to medium sized variable species, distinguished by its transverse corial spots touching inner margin, usually pale venter and dark sixth segment.

I have not seen the type.

Distribution of specimens seen : TIMOR : Dutch-Portuguese Boundary, five miles from coast, 2 ♂, 2 ♀ (*J. E. A. Wahr*); no details, 2 ♀ (*W. Doherty*). TENIMBER : 2 ♂ (*W. Doherty*). TERNATE : 1 ♀. DAMMA I. : 1 ♂. CELEBES : Bankala, 1 ♂ (*J. C. van Hasselt*).

Type locality, Wetter I.

Dysdercus concinnulus Walker, 1872,

concinulus Walker, 1872 : 190 (*Dysdercus*). Blöte, 1931 : 130 in part (as var. of *D. poecilus*). *simplex* Distant (*nec* Walker), 1888 : 485 (*Dysdercus*). *syn. nov.* *variegatus* Distant, 1902a : 42 (*nom. nov.* pro *D. simplex*), *syn. nov.* Bergroth, 1913 : 173 (*Dysdercus*). Hussey, 1929 : 105 (*Dysdercus*). Schmidt, 1932 : 265 (*Dysdercus*). *poecilus* Distant, 1902a : 42 and 45 in part (*Dysdercus*). Bergroth, 1913 : 173 and 1914 : 355 in part (*Dysdercus*). Hussey, 1929 : 99 in part (*Dysdercus*). *incarnatus* Blöte, 1931 : 124 (*Dysdercus*) *syn. nov.*

Antennae: Normal, first segment longer than second. *Rostrum*: Normal, reaches second or base of third abdominal segment. *Anterior femora*: Subapical group of spines only present. *Male genitalia*: Ninth segment upturned apex conical. Parameres of *koenigii* type. Vertical processes distinctive, with strongly marked heads (fig. 49), which in side view are seen to be formed of downwardly projecting hooks—much as in *sidæ* only larger. Second conjunctiva appendages simple. *Spermatheca*: As *koenigii* (fig. 17).

Colour of dorsal surface: Head red, usually darkened apically and behind the eyes. *Prothorax* with white collar, fold and lateral margins orange or red, fold usually darkened both posteriorly and anteriorly, remainder of prothorax greyish-yellow or orange. *Scutellum* red, usually narrowly darkened anteriorly. *Corium* greyish-yellow or orange, costal and apical margins more strongly yellow; black corial spots always absent. *Membrane* dark.

Colour of ventral surface: Red with white fasciae; red often partially or wholly suffused with black. Head red, thorax margined with white as in *superstitiosus* (fig. 1). Abdominal segments 1–6 with white fasciae, in the type narrow but broadened laterally to about half segment width, in the type of *variegatus* (*simplex*) Distant the fasciae of segments 2–5 are broader and forked at the ends as in *olivaceus* (fig. 6); intermediates occur between these two extremes, but most specimens (including the type) show a very slight tendency towards the production of the forwardly projecting tongue.

Legs: Coxae and trochanters pale, femora dark or pale at the base, tibiae and tarsi dark.

Length 10.5–15.5 mm., *breadth across wings* 3.5–5.5 mm.

A small to medium sized species distinguished by absence of markings on corium, presence of a well-marked white fascia on (true) first abdominal segment and often forked fasciae to segments 2–5.

The types of *Dysdercus concinnulus* Walker (a male from Gilolo, coll. Wallace) and *D. simplex* Distant (a female from New Guinea, coll. Sayer) are in the collection of the British Museum. I have not seen the type of *D. incarnatus* Blöte, but from the description, especially the black on the apex of the head, it appears to belong here.

Distribution of the specimens seen: NEW GUINEA: Humboldt Bay District, Pukusan, 5 ♂, 5 ♀, vi.1937 (*W. Stuber*); Mondo, 2 ♂, ii.1934 (*L. E. Cheesman*); Markham V., Kiapit, 2 ♀, ix.1925 (*E. Ballard*); Discovery Bay, 1 ♂; no details, 1 ♂ (*Sayer*).

Type locality: Gilolo.

Dysdercus festivus Gerstaecker, 1892.

festivus Gerstaecker, 1892: 50 (*Dysdercus*). Schouteden, 1912: 304 and 305 (*Dysdercus*). Hussey, 1929: 90 (*Dysdercus*).

Antennae: First antennal segment long, subequal to two and three together; first and fourth subequal. *Rostrum*: Normal, reaches second abdominal segment. *Anterior femora*: Subapical group of spines present only. *Male genitalia*: Ninth segment upturned apex broadly conical. Parameres (fig. 33) of a rather slender *koenigii* type. Vertical processes (fig. 52) quite characteristic. Second conjunctiva processes simple. *Spermatheca* not known.

Colour of dorsal surface. Head, prothorax, scutellum and corium concolorous orange; prothoracic white collar lacking in both the single specimen I have seen and also in the painting of the type (see below); corial fascia not very broad, parallel sided, reaches outer (costal) margin of corium broadly; membrane black.

Colour of ventral surface: General pattern as in *superstitiosus* (fig. 1). Head and thorax orange and white—anterior white collar of prothorax present; abdomen red and white

tinged with orange on the margins; meso- and metapleura darkened on the disc; scent gland spout reddish.

Legs: Coxae, trochanters and femora red, femora apically infuscated; tibiae and tarsi dark.

Length 16.5 mm., *breadth across wings* 5.5 mm. (one specimen only).

A medium sized species easily distinguished by the orange coloration, narrow black corial fascia, absence of prothoracic black fascia and long first antennal segment.

The type, a male from E. Africa, Kikoko, Usaramo, was in the Hamburg Museum. It was borrowed by Mr. W. E. China of the British Museum before the 1939-1945 war, and he fortunately made paintings of lateral and dorsal views. The species can very readily be determined from these paintings.

One specimen only has been seen, a male from Upper Jubaland, Bubasci, collected viii.1984 by Patrizi.

Dysdercus cingulatus (Fabricius, 1775).

cingulatus Fabricius, 1775 : 719 (*Cimex*). Goeze, 1778 : 256 (*Cimex*). Fabricius, 1781 : 364 and 1787 : 299 (*Cimex*). Fabricius, 1794 : 153 and 1803 : 221 (*Lygaeus*). Herrich-Schäffer, 1853 : 177 (*Dysdercus*). Montrouzier, 1855 : 105 (*Lygaeus*). Stål, 1870a : 119 in part and 1870b : 667 (*Dysdercus*). Walker, 1872 : 186 (*Dysdercus*). Distant, 1888 : 484 in part (*Dysdercus*). Carpenter, 1891 : 141 (*Dysdercus*). Kirby, 1891 : 104 in part (*Dysdercus*). Breddin, 1900 : 162, 1901a : 84 in part, 1901b : 19 and 140, and 1901e : 145 (*Dysdercus*). Kirkaldy and Edwards, 1902 : 171 in part (*Astemma*). Distant, 1904 : 118 in part (*Dysdercus*). Breddin, 1905a : 129 and 1905b : 216 (*Dysdercus*). Kirkaldy, 1905 : 346 (*Dysdercus*). Banks, 1909 : 577 (*Dysdercus*). Distant, 1910 : 100 in part (*Dysdercus*). Matsumura, 1913 : 150 (*Dysdercus*). Hussey 1929 : 87 (*Dysdercus*). Blöte, 1931 : 118 (*Dysdercus*).

koenigii Mayr, 1868 : 134 in part (*Dysdercus*). Schmidt, 1932 : 260 in part (*Dysdercus*).

koenigii Burmeister, 1835 : 284 (*Pyrrhocoris*). Blanchard, 1840 : 128 (*Astemma*).

solenis Lethierry, 1883a : 649 ? (as var. of *D. cingulatus*).

ornatus Breddin, 1901a : 85 (as var. of *D. cingulatus*). Horvath, 1919 : 309 (as var. of *D. megalopygus*). Hussey, 1929 : 94 (as var. of *D. megalopygus*).

megalopygus Breddin, 1909 : 300 (*Dysdercus*). Bergroth, 1913 : 173 and 1914 : 355 (*Dysdercus*). Esaki, 1926 : 158 (*Dysdercus*). Taeuber, 1927 : 193 and 195 (*Dysdercus*). Hussey, 1929 : 93 (*Dysdercus*). Schmidt, 1932 : 260 (*Dysdercus*).

Antennae. Normal, first segment longer than the second but not subequal to two and three together. *Rostrum*: Normal, reaches second abdominal segment or sometimes base of third. *Anterior femora*: Subapical group of spines present only. *Proportions of head and prothorax*: Prothorax (fig. 7) narrower posteriorly than *olivaceus*, head smaller in proportion than *poecilus*, lateral margins less strongly sinuate than *decussatus* or almost straight. *Male genitalia*: Ninth segment obviously different from that of any other species, flat, broad and shining, with ventral furrows parallel to margins more or less well developed, and transverse furrow more or less obsolete; apical margin produced into a dorsal longitudinal fold or ridge, appearing conical in apical view. Parameres hooked, can be derived from *koenigii* type by reduction of the folds and crest, quite characteristic and constant in form (fig. 39). Vertical processes broad, closely appressed, narrowed at their tips (fig. 53). Second conjunctiva processes simple. *Spermatheca*: Duct longer than *koenigii*, gland simpler (fig. 18).

Colour of dorsal surface: Head red. Prothorax with collar white, crescent shaped, colour not extending on to lateral margins and rarely on to angles; fold black or red or intermediate, rarely completely red; lateral margins red, concolorous with fold when that is red; disc and posterior margin usually orange but may be pale yellow or a deep reddish colour. Scutellum black. Corium concolorous with disc of prothorax; black corial spots

usually slightly oval, centrally placed and fairly large, but may be much reduced though never completely absent, or enlarged so that they touch one or both margins (var. *ornatus* Breddin), intermediates occurring. *Membrane* dark.

Colour of ventral surface : Red and white, often but not always with a variable amount of black suffusing the red particularly on the thorax ; occasionally red entirely replaced by black except on head, part of sixth abdominal segment and a very narrow margin to abdomen ; dark specimens do not necessarily have broad or very broad corial spots, though in these specimens the spots are always well developed. Head and thorax as in *superstitiosus* (fig. 1) ; segments 1-6 of abdomen with white posterior fasciae, variable in size ; fasciae on segments 2-4 often quite narrow but may be broadened laterally to half segment width or more, always narrowed ventrally ; fasciae on segments 1 and 5, as usual, narrower ; segment 6 bears normal crescent-shaped fascia.

Legs : Coxae and trochanters red, femora completely black or basally red, very rarely entirely red, tibiae and tarsi black or dark.

Length 12-18 mm., *breadth across wings* 3.5-5.5 mm.

A fairly large species occurring in eastern India and extending to the Pacific Is., China and Australia ; separable from *koenigii* by its distribution, usually dark femora and prothoracic fold, and by its genitalia ; separable from *sidae* by its fasciated abdomen, by the clearly crescentic prothoracic collar with the white not, or rarely, extending on to the anterior angles, and by the genitalia ; separable from *poecilus* when the corial fascia is somewhat similar, by the presence of a clear white fascia on the first abdominal segment, by the prothoracic white collar, and by the genitalia.

I have seen the type, a female from Australia, in the Banks Collection in the British Museum.

Distribution of specimens seen : BENGAL : Chittagong, 1 ♂ (*H. M. Parrish*). ASSAM : Khasia Hills, 2 ♂, 2 ♀ ; Naga Hills, 2 ♂, 6 ♀ ; Mishmi Hills, Delai V., 1 ♀, xi.1936 (*M. Steele*). BURMA : Mishmi Hills, 1 ♀ (*M. Steele*) ; Kachin Hills, 1 ♀, xii.1930 (*Kingdon-Ward*) ; Pegu, 1 ♀ ; Rangoon, 1 ♀ ; Amherst, 1 ♂ ; Tavoy I., 1 ♀ (*Atkinson*). SIAM : Bangkok, 2 ♂, 2 ♀, xi.1919 (*F. J. Godfrey*) ; Nan, 1 ♀ (*M. M. Collier*). FRENCH INDO-CHINA : Vientiane, 2 ♂, 9 ♀, iv.1919 ; Ban Nam Kum, 1 ♂, x.1916 ; Hoabinh, 1 ♂, 3 ♀, i.1917 ; Luang Prabang, 2 ♂, ix.1917 ; Muong Sing, 1 ♀, iv.1918 ; Chieng Kwang, 1 ♂, 1 ♀, iv.1919 ; Tonkin, 10 ♂, 6 ♀ (all coll. *R. V. de Salvaza*) ; Bao Ha, 1 ♂, xii.1923 (*H. Stevens*) ; Thai Nien, 6 ♂, 5 ♀ (*H. Stevens*). HAINAN : Wuteryang, 1 ♂, v.1903 ; Mt. Wuchi, 3 ♂, 1 ♀, v.1904 ; Hengron, 1 ♂, 2 ♀, vi.1904 ; Mangrin, 1 ♀, vi.1904 ; You Boi, 10 ♂, 14 ♀, vi.1904 ; Porten, 1 ♀, viii.1904 ; no details, 1 ♂, 1 ♀. CANTON : Honan I., 3 ♂, iii.1926 (*W. E. Hoffman*) ; Hong Kong, 2 ♂. "YANGTZE" : 1 ♂, 1 ♀. FORMOSA : Tamsin, 2 ♀ (*J. de la Touche*). MALAY STATES : Perak, 2 ♂, 1 ♀ ; Taiping, 1 ♀ (*W. B. Orme*) ; Selangor, 1 ♂ (*H. E. Durham*), 1 ♂, 1 ♀ (*C. J. Brooks*) ; Klang, 6 ♂, 5 ♀, vi.1910 ; Kuala Lumpur, 4 ♂, 1 ♀, i.1921 (*W. A. Lamborn*) ; Bukit Kutu, 2 ♂, 2 ♀ (*A. R. Sanderson*) ; Singapore, 2 ♂, 1 ♀. SUMATRA : Fort de Kock, 1 ♀ (*E. Jacobson*) ; Medan, 1 ♀ (*J. B. Corporaal*). JAVA : Buitenzorg, 2 ♀, 1877 (*G. B. Ferrari*) ; Tjigomborg, 1 ♀ (*C. W. Andrews*) ; Kederi, 1 ♀. BALI : Danan Bratan, 1 ♀ (*E. Stresemann*) ; no details, 1 ♂. BORNEO : Sarawak, 6 ♂, 5 ♀ (*C. J. Brooks*), 1 ♂, 1 ♀ (*J. E. A. Lewis*), foot of Mt. Dulit, 4 ♂, 6 ♀, vii.1932 (*Hobby and Moore*) ; Sandakan, 7 ♂, 4 ♀ (*Cator*

and Creagh); Pulo Laut, 1 ♂ (*Gribodo*). PHILIPPINE IS.: Mindoro, Baco R., 1 ♂, x.1909; Manila, 8 ♂, 5 ♀ (*E. Simon*); no details, 5 ♂, 3 ♀. CELEBES: Toli Toli, 1 ♀, xi.1895 (*H. Fruhstorfer*); Palu, 1 ♂, 3 ♀; Bankala, 1 ♂ (*J. C. van Hasselt*); no details, 1 ♂, 4 ♀. MOLUCCAS: Ternate, 1 ♀; Obi, 2 ♀; Ceram, 2 ♀; Amboina, 1 ♀. KEY IS.: 1 ♂, 1 ♀, ix.1874. TENIMBER: 1 ♂ (*W. Doherty*). NEW GUINEA: Rorona, 2 ♂, 1 ♀, viii.1925 (*E. Ballard*); Goodenough I., 5 ♂, 2 ♀, ix.1925 (*E. Ballard*); Humboldt Bay, 2 ♂, 2 ♀, iv-vi.1936 (*L. E. Cheesman*); no details, 1 ♂. NEW IRELAND: 1 ♀. SOLOMON IS.: Guadalcanal, 1 ♀ (*R. A. Lever*). NEW CALEDONIA: 1 ♀ (*A. Gambey*). AUSTRALIA: Northern Territory, Melville I., 1 ♀, Bathurst I., 2 ♀, and 1 ♀ (*G. F. Hill*); Queensland, Torres Strait, 2 ♂, 2 ♀, and 1 ♂ (*Kelsall*), 1 ♀ (*Mackey*); South Australia, Adelaide River, 1 ♀.

Ballard (1927: 298) states that this species exists in two forms in New Guinea, a spotted and a banded form, with the latter apparently preferring a wetter climate. It is possible, as suggested by Golding (1928: 319), that these forms are similar to the forms of *D. superstitiosus* (see under that species).

Dysdercus sidae Montrouzier, 1861.

sidae Montrouzier, 1861: 68 (*Dysdercus*). Stål, 1870a: 120 (*Dysdercus*). Walker, 1872: 188 (*Dysdercus*). Kirkaldy, 1905: 345 (*Dysdercus*). Distant, 1914b: 383 and 1920: 155 (*Dysdercus*). Blöte, 1931: 132 (*Dysdercus*).

insularis Stål, 1870a: 120 (*Dysdercus*), *syn. nov.* Walker, 1872: 188 (*Dysdercus*). Kirkaldy, 1908: 354 (*Dysdercus*). Hussey, 1929: 92 (*Dysdercus*). China, 1930: 140 (*Dysdercus*). Blöte, 1931: 127 (*Dysdercus*).

biguttatus Walker, 1873: 11 (*Dindymus*) *syn. nov.* Distant, 1902a: 42 and 44 (*Dysdercus*). Bergroth, 1913: 172 (*Dysdercus*). Hussey, 1929: 86 (*Dysdercus*).

cingulatus Kirkaldy and Edwards, 1902: 171 in part (*Astemma*). Bergroth, 1914: 355 (*Dysdercus*). Hussey, 1929: 87 in part (*Dysdercus*). Schmidt, 1932: 261 in part (*Dysdercus*).

rubricutellatus Breddin, 1901c: 11 (*Dysdercus*) *syn. nov.* Bergroth, 1913: 173 (*Dysdercus*). Hussey, 1929: 100 (*Dysdercus*).

remotus Distant, 1914b: 383 (*Dysdercus*). Hussey, 1929: 100 (*Dysdercus*).

concinulus Blöte, 1931: 130 in part (as var. of *D. poecilus*).

Antennae: Normal, first segment longer than second but not as long as two and three together. *Rostrum*: Longer than in most species, reaches at least to third and often to apex of fourth abdominal segment; segment proportions normal. *Anterior femora*: Sub-apical spines present only. *Male genitalia*: Quite characteristic. Ninth segment with finger-like dorsal apical process (figs. 11 and 12) set back from apex. Parameres (fig. 40) at apex broadened laterally to a wing-like lobe on the outer side. Vertical processes (figs. 11, 12 and 54) long, slender and curved over at the tips but not so strongly as in *coenigii* and *cingulatus* (figs. 17-18).

Colour of dorsal surface: Head red with often an apical black spot either on central lobe alone or on all three lobes and also may be darkened behind the eyes. *Prothorax* with whitish collar, the colour extending to the anterior angles (compare *cingulatus*) and the collar often narrow, not crescent-shaped; anterior fold typically black, but may be red in the light specimens mentioned below, or intermediate; lateral margins reddish; disc and posterior margin pale ochraceous, orange or red. *Scutellum* black, in lightest forms red or intermediate. *Corium* concolorous with disc of prothorax, black corial spots circular, centrally placed, very variable in size. I have seen no specimens in which they are missing, but several with them practically absent. *Membrane* dark.

Colour of ventral surface : In most specimens whitish and black with head red, see under "Colour variation" below for the other forms. Thorax fasciated as in *superstitiosus* (fig. 1), but red mainly replaced or suffused with black except on prothorax, which retains some of its red. Abdominal segments 1-5 mainly white ; segments 2-4 anteriorly black, sometimes narrowly black, sometimes widely, causing belly to appear fasciated as in other species only with black and white instead of red and white ; segment 6 black except at the apex where it is whitish ; segment 5 either as segments 2-4 or almost entirely black as segment 6 ; genitalia reddish, black apically in the male ; margin of abdomen reddish.

Legs : Coxae and trochanters red, femora red or black or red with the apices black, tibiae and tarsi dark.

Length 8-14.5 mm., *breadth across wings* 2.5-5.0 mm.

Colour Variation.

All the black except the corial spots may be replaced by red. In the British Museum collection light specimens of this type are more frequent from Australia (*D. biguttatus* (Walker)), but there are similar specimens from Samoa and New Hebrides and intermediates occur. In some specimens from several localities the white on the venter is flushed with pale orange, which also causes the black of segment 6 to retreat (Stål's character for *D. insularis*) ; it is possible that this variation is similar to the one recorded in *superstitiosus* by Pomeroy (see under that species).

A small to medium sized species with an Australasian distribution, distinguishable from *D. poecilus* by the wholly or partially white (true) first ventral abdominal segment, from *D. cingulatus* by the narrow prothoracic white collar, the colour extending to the anterior angles and from these and all other species by the distinctive male genitalia.

Synonymy.

I have not seen Montrouzier's type of *D. sidae*, but his description mentions a black spot apically on the head and behind each eye, that the abdomen is white fasciated with black and the thorax black annulated with white. This description agrees with the above-described species and with no other that I have seen. Stål's description of *D. insularis* agrees with the form with the yellowish venter ; so far as can be gathered from both the collection and the literature, only two species (*D. oceanicus* and this one) are known from Fiji, which is extra evidence for regarding Stål's species as a synonym. The type of Walker's *Dindymus biguttatus*, which is a light female from Pt. Essington, N. Australia, and a cotype of Distant's *Dysdercus remotus*, a small male from the Loyalty Is., are both in the collection of the British Museum and both undoubtedly belong to this species. Breddin's species *D. rubriscutellatus* has been considered by Hussey (1929) to be a distinct species and by Blöte (1931) as a synonym for *concinulus* Walker which he thought to be a variety of *D. poecilus*. I have not seen the type and the description is vague, but from the length of the rostrum (reaching to the third segment) it seems probable that it belongs here and is not a synonym of *D. poecilus* : a final decision must await an examination of the type.

Distribution of the specimens seen : NEW SOUTH WALES : Biloela, = 2 ♂
1 ♂, iii.1925 ; no details, 3 ♂, 3 ♀ (*W. B. Gurney*). QUEENSLAND : Rock-
hampton, 1 ♀, iii.1924 (*G. H. Wilkins*), and 1 ♂, 1 ♀ ; Thursday I., 1 ♀
(*F. Hartzer*). NORTHERN TERRITORIES : Bathurst I., 1 ♀ ; Darwin, 2 ♀
(*G. F. Hill*) ; Port Essington, 1 ♀ ; no details, 3 ♂, 3 ♀. NEW GUINEA :
Higiū, 2 ♂, 1 ♀, viii.1925 (*E. Ballard*) ; Markham V., 1 ♂, 2 ♀, ix.1925
(*E. Ballard*) ; Njau-limon, Mt. Bougainville, 4 ♂, 3 ♀, ii.1936 (*L. E.*
Cheesman) ; no details, 1 ♀ (*Sayer*). SOLOMON IS. : Guadalcanal, 5 ♂,
5 ♀, 1930 (*R. A. Lever*). NEW HEBRIDES : Espiritu Santo, 1 ♀, 1910
(*S. F. Speiser*) ; Malekula, Ounua, 15 ♂, 6 ♀, ii-iv.1929, Malua Bay, 3 ♂,
2 ♀, vi.1929, no details, 4 ♂, 1 ♀, xii.1929 (*L. E. Cheesman*) ; Aneityum,
5 ♂, 4 ♀, xi.1930 (*L. E. Cheesman*) ; Tanua, 1 ♂, ix.1930 (*L. E. Chees-*
man) ; Erromanga, 2 ♀, vii.1930 (*L. E. Cheesman*) ; no details, 1 ♂
(*P. Francoise*). NEW CALEDONIA : Koné, 1 ♀, viii.1911 ; Houadou R.,
1 ♀, xi.1914 ; Muao, 1 ♂, 1 ♀, v.1927 (*T. D. A. Cockerell*) ; no details,
2 ♂ (*Lethierry*) and 6 ♂, 6 ♀ (*P. D. Montague*). LOYALTY IS. : Maré,
1 ♂, 1 ♀, xi-xii.1911 ; no details, 1 ♀. FIJI : Levuka, 1 ♂, 1 ♀, v.1921
(*H. W. Simmonds*) ; Waikia, 1 ♂, 1 ♀, x.1880 ; Labasa, 1 ♂, 1 ♀, x.1914
(*R. Veitch*)—noted as very numerous. TONGA : Savage I. (Alofi), 1 ♀ ;
Tongatabu, 2 ♂. SAMOA : Upolu, 8 ♂, 6 ♀, xi-xii.1922 (*J. S. Armstrong*) ;
Upolu, 3 ♂, 1 ♀, iv.1924 and 2 ♂, 4 ♀, xi.1924 (*Buxton and Hopkins*) ;
Monomo, 1 ♂, 4 ♀, vi.1924 (*Buxton and Hopkins*) ; Savaii, 1 ♂, 1 ♀,
xi.1925 (*Buxton and Hopkins*) ; no details, 1 ♀, 1921 (*F. W. O'Connor*).

Type locality : New Caledonia.

A full account of the biology of this species in Queensland is given by
Ballard and Evans (1928).

Dysdercus longiceps Breddin, 1901.

longiceps Breddin, 1901c : 11 (*Dysdercus*). Bergroth, 1913 : 173 (*Dysdercus*). Hussey,
1929 : 93 (*Dysdercus*).

Antennae : First segment shorter than in the other species, not reaching beyond apex of
head, slightly shorter than second segment. *Rostrum* : Long, reaching to third or base of
fourth abdominal segment. *Head* as long as prothorax, swollen. *Anterior femora* : In
addition to subapical group of spines there are usually a few extra small spines on the apical
half. *Male genitalia* : Ninth segment with upturned apex small and conical. Parameres
(fig. 41) quite characteristic, apical fold exaggerated, transverse crest reduced. Vertical
processes widely separated and pointed (fig. 55). Second conjunctiva appendages simple.
Spermatheca : As *koenigii* (fig. 17).

Colour of dorsal surface : Head completely black in two specimens, reddish behind
antennae in other two specimens (in each case one from each locality) ; prothorax com-
pletely red except for a dark elliptical suffusion posteriorly ; scutellum black ; corium red,
corial black spots large or small, may touch outer margin ; membrane dark.

Colour of ventral surface : Head dark or reddish posteriorly ; thorax with usual white
epimera (see fig. 1), red sometimes darkened ; abdominal segments 1-6 red with white
apical fascia not noticeably wider laterally and narrower than half segment width ;
abdominal incisures not black.

Legs : Coxae and trochanters red, femora, tibiae and tarsi black or dark, femora may
be reddish basally.

Length 11-14 mm., *breadth across wings* 3.5-4.5 mm.

A small to medium sized species readily distinguished by large head, short first antennal segment, dark posterior ellipse on prothorax and narrow parallel-sided white fasciae of abdomen.

I have not seen the type.

Distribution of specimens seen: TORRES STRAIT: Cornwallis I., 2 ♀. AUSTRALIA: Port Darwin, 1 ♂, 1 ♀.

Type locality: Cornwallis I.

Dysdercus argillaceus Bergroth, 1895.

argillaceus Bergroth, 1895: 293 (*Dysdercus*). Breddin, 1901c: 91 (*Dysdercus*). Bergroth, 1913: 172 (*Dysdercus*). Hussey, 1929: 86 (*Dysdercus*).
sordidulus Breddin, 1901c: 12 (*Dysdercus*).

Antennae: Segment one subequal to two and three together; segment four yellowish ochraceous, other segments dark or brown. *Rostrum*: Normal, reaches second abdominal segment. *Anterior femora*: Subapical spines rather long, usually a few small spines scattered along the length. *Prothoracic margins*: Lateral margins sinuate and rounded as in *decussatus* (fig. 10), anterior margin less than half width of posterior margin. *Scutellum*: With strong basal punctures. *Male genitalia*: Ninth segment with apical margin simple, only the very slightest indication of a callosity on the dorsal surface. Parameres of the typical *koenigii* type. Vertical processes long and narrow, closely appressed and with straight shoulders (fig. 56), very similar in general structure to those of *oceanicus* but distinguished by the shoulders. Second conjunctiva appendages forked as in *decussatus* (fig. 14). *Spermatheca*: As *mesostigma* (fig. 20), though duct longer.

Colour of dorsal surface: Head, prothoracic fold and scutellum pink or red, prothoracic collar white, membrane dark, remainder of surface fairly uniform grey; no black corial spots.

Colour of ventral surface: Head and thorax pale red and white with pattern as in *superstitiosus* (fig. 1). First (true) abdominal segment grey; segments 2-3 with red basal crescentic fasciae, segments 4-6 mainly red, only grey apically; red may be replaced laterally by yellow or grey, the final effect being of a ventral red crescent on each segment.

Legs: Uniformly pale, with last tarsal segment and claws dark or black.

Length 12.5-16 mm., *breadth across wings* 3.5-5 mm.

A medium sized species with pale dorsal surface, no corial markings, pale terminal antennal segment and red and grey ventral fasciae.

I have not seen the type.

Distribution of specimens seen: NEW GUINEA: Kokoda, 1 ♂, 2 ♀, ix.1933 (L. E. Cheesman). TORRES STRAIT: Cornwallis I., 3 ♀.

Type locality: Queensland.

Dysdercus oceanicus Boisduval, 1835.

oceanicus Boisduval, 1835: 641 (*Dysdercus*). Stål, 1870a: 124 (*Dysdercus*). Walker, 1872: 189 (*Dysdercus*). Hussey, 1929: 97 (*Dysdercus*).

✓ *impictiventris* Stål, 1870: 120, (*Dysdercus*) syn. nov. Walker, 1872: 188 (*Dysdercus*). Distant, 1902a: 42 (*Dysdercus*). Kirkaldy, 1908: 354 (*Dysdercus*). Bergroth, 1913: 173 (*Dysdercus*). Hussey, 1929: 91 (*Dysdercus*). China, 1930: 140 (*Dysdercus*). Schmidt, 1932: 265 (*Dysdercus*).

albescens Walker, 1872: 190 (*Dysdercus*).

Antennae: First segment subequal to two and three together. *Rostrum*: Normal, reaches second segment. *Prothorax*: Not strongly sinuate, sometimes almost straight laterally; shining, punctation sparse but individual punctures coarse. *Anterior femora*: Subapical spines rather long as in *argillaceus*; indications of a few small spines along the

length. *Scutellum* : With strong sparse punctures basally, the punctures being of the same size as those on the hemelytra. *Male genitalia* : Ninth segment with upturned apex broadly rounded ; external transverse impression shallow or absent. Parameres of *koenigii* type. Vertical processes (fig. 57) long, closely appressed, apically rounded, similar to *argillaceus* but distinguished by rounded shoulders. Second conjunctiva appendages forked (fig. 14). *Spermatheca* : As *decussatus* (fig. 19), gland more as *mesostigma* (fig. 20).

Colour of dorsal surface : Variable ; head black or red or intermediate ; prothoracic collar white or reddish, fold reddish, remainder of prothorax grey, sometimes suffused with black or yellow, lateral margins sometimes yellow or with a very fine dark edge ; scutellum red ; corium unspotted, pale or dark grey ; membrane dark.

Colour of ventral surface : Variable ; head black or orange-red ; thorax yellow, orange or red with usual white epimera (fig. 1) ; abdomen pale yellow with a variable amount of red suffusion, margins always red, apical segment always red, but red often spreads on to segments 5 or 6 and in the true *oceanicus* of Boisduval suffuses the whole abdomen.

Legs : Coxae, trochanters and normally femora except extreme tips, orange ; tibiae, tarsi and tips of femora black or brown, sometimes entire femora brownish.

Length : 10–14 mm., *breadth across wings* 3.5–4.5 mm.

Variation and Synonymy.

So far as can be judged from the limited number of specimens examined, this species shows quite well-marked geographical variation. The specimens from the Solomons are paler, have a totally red venter and stronger punctation of the thorax, and are undoubtedly the same as the specimens originally examined by Boisduval from New Ireland. The Fiji specimens on the whole are darker on the dorsal surface, particularly on the head, but are paler ventrally, whilst the Samoan specimens have the head and thorax much more orange. These are *D. impictiventris* of Stål and *albescens* of Walker (the type of the latter is in the British Museum). There is no well-defined difference and the male genitalia of all three forms are identical ; I have, therefore, considered them to be one and the same species.

I have not seen the type.

Distribution of specimens seen : SOLOMON Is. : Guadalcanal, 2 ♂, x–xii.1931 (*R. A. Lever*). FIJI Is. : Vanua Balavu, Loma Loma, 1 ♀, viii.1921 (*H. S. Evans*) ; Viti Levu, Mokogai, 1 ♂, 1 ♀, i.1921 (*H. S. Evans*) ; Viti Levu, 1 ♂, 2 ♀, vi.1915 (*R. Veitch*) ; Taviuni, 1 ♀, x.1923 (*H. S. Evans*) ; no details, 1 ♂, 3 ♀. SAMOAN Is. : Upolu, Apia, 2 ♂, 1 ♀, xi.1924 (*J. S. Armstrong*) and 2 ♂, 2 ♀, x.1924 and 3 ♂, 2 ♀, iv.1924 (*Buxton and Hopkins*) ; Upolu Vailima, 2 ♂, 1 ♀, vi.1924. (*Buxton and Hopkins*) ; Tutuila, Pago Pago, 1 ♂, xii.1924 (*Buxton and Hopkins*).

Type locality : New Ireland.

Dysdercus mesostigma Distant, 1888.

mesostigma Distant, 1888 : 484 (*Dysdercus*). Breddin, 1900 : 162 (*Dysdercus*—subg. *Megadysdercus*). Kirkaldy and Edwards, 1902 : 172 (*Astemma*). Distant, 1904 : 120 (*Dysdercus*). Breddin, 1905b : 216 (*Dysdercus*). Distant, 1914a : 343 (*Dysdercus*). Tauer, 1927 : 190 and 195 (*Dysdercus*). Hussey, 1929 : 106 (subg. *Megadysdercus*). Blöte, 1931 : 133 (*Dysdercus*).

Antennae : First segment usually subequal to second, but it may be a little longer or a little shorter than the second. *Rostrum* : very long ; reaches at least to base of fifth and sometimes to apex of sixth abdominal segment ; second segment slightly longer than first,

third often nearly twice as long as fourth, always elongate. *Prothorax*: Lateral margins strongly rounded and sinuate as *decussatus* (fig. 10). *Sculpture and pubescence*: Prothorax less strongly punctured than is usual and punctures finer. Entire dorsal and ventral surfaces hirsute—a unique character amongst the non-American species at any rate; prothoracic fold and scutellum closely and finely pubescent, remainder of surface much more sparsely hirsute; scutellum lacking the strong basal punctures of the other species of this group. *Anterior femora*: Short spines present, distributed sparsely along the length ventrally, in addition to the usual subapical group. *Male genitalia*: Ninth segment with upturned apex conical in terminal view, flattened in vertical plane in lateral view. Parameres (fig. 42) somewhat intermediate between *koenigii* and *decussatus* types. Vertical processes (fig. 58) broad, more or less pointed and slightly divergent, in general structure similar to those of *decussatus*. Second conjunctiva appendages forked. *Spermatheca*: Resembles *decussatus* but duct shorter and gland more enlarged at apex (fig. 20).

Colour of dorsal surface: Head, prothorax, scutellum and corium uniform in colour but varying from grey ochraceous to deep red; occasionally in lighter forms margins of prothorax and corium reddish and prothoracic fold may be darker; base of scutellum narrowly black, no dark markings of any kind on the corium; pale specimens may have segments 1-3 of the antennae pale; membrane pale with a large irregularly shaped black spot basally across, but not in, the anal angle.

Colour of ventral surface: Entire surface varies from a very pale pink or ochraceous to deep red without much regard to colour of dorsal surface, except that forms with a red dorsal surface have a red ventral surface. White epimera and coxal cavities reduced but usually discernible; meso- and sometimes metapleuron black anteriorly; abdominal segments 2-4 with or without broad black bands occupying much of apical half of segments, apical margins of segments 2-5 laterally narrowly pale.

Legs: Very variable; may be completely red, pale or black, or have red femora with black tibiae and tarsi, or the femora may be only partially red.

Length 17-24 mm., *breadth across wings* 5.5-7.5 mm.

A large species easily recognised by its immaculate corium, pale membrane with black basal spot, very long rostrum and pubescent surface.

Type, a female from New Guinea, in the collection of the British Museum.

Distribution of specimens seen: CEYLON: Kandy, 1 ♀, xii.1907; Madulsima, 1 ♀, i.1909; (*T. B. Fletcher*) no details, 1 ♂, 1 ♀ (*Green*) and 6 ♂, 6 ♀ (*G. W. Bury*). CHINA: Amoy, 1 ♀; Hong Kong, 1 ♂. MALAY STATES: Selangor, 1 ♂, 2 ♀, x.1924 (*Corbett and Gater*). Bukit Kutu, 1 ♂ (*A. R. Sanderson*). BORNEO: Sanga Sanga, 1 ♀ (*H. D. Jensen*); N.W. Borneo, 1; Sarawak, Mt. Dulit, 1 ♀, ix.1932 (*Hobby & Moore*); LETI I.: 1 ♀ (*W. Doherty*). SALAYER I.: 1 ♂, 1 ♀ (*Everitt*). AMBOINA: 2 ♂, 2 ♀, xi.1923. (*C. J. Brooks*). NEW GUINEA: Ekeikei, 1 ♂, iv. 1903 (*Pratt*); Cyclops Mts., Sabron, 1 ♀, vii.1936 (*L. E. Cheesman*); Humboldt Bay District, 3 ♂, 3 ♀ (*W. Stuber*); Dore, 2 ♀ (*Wallace*); no details, 1 ♀ (*Sayer*). SOLOMON IS.: Bougainville, 1 ♀.

Dysdercus philippinus Herrich-Schäffer, 1853.

philippinus Herrich-Schäffer, 1853: 176 (*Dysdercus*). Mayr, 1868: 134 (*Dysdercus*). Stål, 1870a: 118 and 1870b: 667 (*Dysdercus*). Walker, 1872: 188 (*Dysdercus*). Distant, 1888: 484 (*Dysdercus*). Tauber, 1927: 190 and 195 (*Dysdercus*). Hussey, 1929: 99 (*Dysdercus*). Schmidt, 1932: 263 (*Dysdercus*).

Antennae: First segment subequal to two and three together. *Rostrum*: Normal, reaches apex of second or base of third abdominal segment. *Prothorax*: Not strongly sinuate

laterally in the specimens that I have seen, but anterior margin less than half the width of posterior margin. *Anterior femora*: Subapical group of spines only present (compare with the smaller species *decussatus*). *Scutellum*: Strong, sparse, basal punctures present. *Male genitalia*: Not known. *Spermatheca*: As *mesistigma* (fig. 20).

Colour of dorsal surface: Of the three specimens seen, two have red coloration, one has the red replaced by yellow. Head black; prothoracic collar white, in one specimen remainder of prothorax is red, in the other two it is red or yellow darkened on the disc posteriorly; scutellum red or yellow; clavus and corium black, corium has a white band along claval suture and apical margin, forming a St. Andrew's cross when the wings are closed; posterior arms of cross strongly widened to costal margin, costal margin pale; membrane dark.

Colour of ventral surface. Red or yellow and white. Head pale; thorax with white epimera and coxal cavities as in *superstitiosus* (fig. 1); abdominal segments 1-5 with white apical fasciae not or scarcely broadened laterally, less than half width of segment, fourth being one-third as wide, fifth a quarter as wide; sixth segment apically and margin of abdomen obscurely pale.

Legs: Coxae red or yellow, trochanters red or yellow darkened ventrally, femora pale at extreme base dorsally, remainder of leg black.

Length 18 mm., *breadth across wings* 6 mm. (three specimens).

A large species with a white St. Andrew's cross, the posterior arms of which are strongly broadened, and the anterior femora bear subapical spines only.

I have not seen the type.

Distribution of specimens seen: PHILIPPINE IS.: Mindoro, Baco R., 1 ♀, x.1909 (*J. J. Mounsey*); no details, 1 ♀, 1925 (*E. M. Ledyard*). No locality label, 1 ♀.

Type locality: Philippine Is.

Dysdercus decussatus Boisduval, 1835.

decussatus Boisduval, 1835: 640 (*Dysdercus*). Stål, 1870a: 124 (*Dysdercus*). Walker, 1872: 189 (*Dysdercus*). Distant, 1888: 484 (*Dysdercus*). Hussey, 1929: 89 (*Dysdercus*).

cruciatus Montrouzier, 1855: 106 (*Lygaeus*) syn. nov. Stål, 1870a: 124 (*Lygaeus*). Bergroth, 1913: 172 (*Dysdercus*). Hussey, 1929: 88 (*Dysdercus*). Blöte, 1931: 121 (*Dysdercus*).

fabricii Montrouzier, 1855: 106 (*Lygaeus*). Stål, 1870a: 124 (*Lygaeus*).

crucifer Stål, 1870a: 118 (*Dysdercus*) syn. nov. Walker, 1872: 189 (*Dysdercus*). Kirkaldy and Edwards, 1902: 172 (*Astemma*). Matsumura, 1913: 151 (as new species *Dysdercus*). Bergroth, 1914: 354 (*Dysdercus*). Horváth, 1914: 660 (*Dysdercus*). Esaki, 1926: 158 (*Dysdercus*). Hussey, 1929: 88 (*Dysdercus*). Blöte, 1931: 121 (*Dysdercus*) Schmidt, 1932: 262 and 263 (*Dysdercus*).

simplex Walker, 1873: 6 (*Dindymus*) syn. nov. Distant, 1902a: 42 and 44 (*Dysdercus*). Distant, 1904: 121 (*Dysdercus*). Bergroth, 1913: 173 (*Dysdercus*). Hussey, 1929: 103 (*Dysdercus*). Schmidt, 1932: 263 (*Dysdercus*).

papuensis Distant, 1888: 484 (*Dysdercus*). Carpenter, 1891: 140 (*Dysdercus*).

decorus Breddin, 1901b: 19 and 82 (*Dysdercus*). Breddin, 1901d: 115 (*Dysdercus*). Schmidt, 1932: 263 (*Dysdercus*).

simon Taeuber, 1927: 190 and 195 (*Dysdercus*) syn. nov. Hussey, 1929: 103 (*Dysdercus*). Blöte, 1931: 132 (*Dysdercus*). Schmidt, 1932: 263 and 265 (*Dysdercus*).

jacobsoni Blöte, 1931: 127 (*Dysdercus*) syn. nov.

sumatranus Schmidt, 1932: 263 (*Dysdercus*) syn. nov.

sauteri Schmidt, 1932: 263 and 264 (*Dysdercus*) syn. nov.

Antennae: First segment subequal to two and three together. *Rostrum*: Normal, reaches second abdominal segment. *Prothorax*: Lateral margins strongly sinuate (fig. 10);

anterior margin less than half as wide as posterior margin; anterior angles rounded so that thorax not touching eyes, as in the figure, or produced to touch eyes, with all intermediates. *Scutellum*: With strong sparse punctures basally. *Anterior femora*: In addition to sub-apical group, spines are present along their length (compare *philippinus*). *Male genitalia*: Ninth segment with a fairly narrow bilobed upturned apex. *Parameres* (fig. 43) derived from *koenigii* type by exaggeration of apical fold and reduction of transverse crest. Vertical processes (fig. 59) more or less narrowed to apex, usually divergent, reminiscent of those of *mesio stigma*. Second conjunctiva appendages forked (fig. 14). *Spermatheca*: Duct longer and gland narrower (fig. 19) than *mesio stigma*.

Colour of dorsal surface: Very variable. *Head* red or black or intermediate; all grades may occur in each locality. *Prothorax* with collar white or obscurely white; anterior fold usually red, but may be black (*crucifer* Stål) or intermediate; lateral margins red or pale; disc red, yellow or black; posterior margin usually narrowly pale. *Scutellum* usually black, but some specimens show a reddish colour or are intermediate (*simplex* Walker). *Clavus* usually black but may be obscurely red in some red forms. *Corium* black in true *decussatus* Boisduval with narrow pale costal margin and only an occasional indication of a St. Andrew's cross; red in forms *simplex* Walker and *crucifer* Stål with a clear white cross; all stages between these two extremes occur—*papuensis* Distant was described from a black form with a clear white cross and many red specimens show a progressive darkening of the corium; some Amboina specimens show an all-grey corium with no cross but with clavus and scutellum black, a small Philippine specimen shows clavus and corium yellowish-grey, scutellum dark, the Ceylon specimen is uniform red on the dorsal surface with no cross. *Membrane* always dark. St. Andrew's cross when present formed by white stripes on the coria along the claval sutures and apical margins, posterior arms of cross never strongly widened to costal margin, but often attenuated.

Colour of ventral surface: Variable, but much less so than dorsal surface. Typically red and white, but some very dark forms have the red mostly replaced by black. *Head* usually, but not always, pale; *thorax* with white epimera, coxal cavities and prothoracic collar as usual; *abdomen* nearly always with white fasciae on some or all of segments 1-6; fasciae narrow and hardly broadened laterally, less than half as wide as segment; fasciae often missing from segments 5 and 6 and sometimes only present on segments 2 and 3. *Meso- and metathorax* often darkened, but darkening may spread over all the red of ventral surface except the abdominal margins.

Legs: May be all black, or coxae, trochanters and femora red, tibiae and tarsi black or brown.

Length 11-15.5 mm., *breadth across wings* 3-5.5 mm.

A medium sized species distinguished by absence of transverse corial markings, usual presence of an X-cross on the coria not posteriorly widened, presence of spines along the anterior femora, shape of thorax and presence of white fasciation of the venter.

Synonymy and Variation.

This species is one of the most variable, if not the most variable, in the genus, and many of its main varieties have been described as species. I have seen the types of *Dindymus simplex* Walker and *Dysdercus papuensis* Walker and some specimens collected by Sauter at the same date and locality as specimens described by Schmidt (1932) as *D. sauteri*; all are in the British Museum. Although I have not seen the types, it is quite easy to pick specimens corresponding to all the synonyms given above. All the forms are linked by intermediates, and so far as can be seen there are no structural differences whatsoever to be found

between any of them; for this reason I am considering all the forms to belong to one and the same species. *D. philippinus* appears to be a distinct species, because of the absence of spines along the anterior femora; this is a character of particular importance because it is a larger species than *decussatus* and large specimens usually have these spines better developed. Specimens from the true Oriental Region, including Celebes, appear to be far more red than those from the Australasian Region; the New Guinea and Australian specimens tend to be black with a white cross, those from farther east—Solomons and New Hebrides—tend to be dark without the white cross.

Distribution of specimens seen: CEYLON: 1 ♀ (*Green*). SIKKIM: 1 ♀ (*Atkinson*) (locality correct?). NICOBAR IS.: 5 ♂, 5 ♀ (*G. Rogers*); 1 ♂, 1 ♀ (*Atkinson*). ANDAMAN IS.: Rutland Is., 1 ♂, iii.1904 (*G. Rogers*). MALAY PENINSULA: 1 ♀ (*Champion*); Dindings, 1 ♀. SUMATRA: Doerian Moelan, Brindjei, 1 ♂ (*R. Coughtrie*); Lebong Tandai, 1 ♀ (*C. J. Brooks*); Sinkep I., 2 ♀ (*Atkinson*). BORNEO: Sarawak, foot of Mt. Dulit, 1 ♂, ix.1932 (*Hobby and Moore*); N. Borneo, 1 ♀. PHILIPPINE IS.: 2 ♂, 2 ♀. CHINA: Hainan, Koniya, 1 ♂, viii.1904; Shensi, Tai-paishan, 1 ♀, viii.1904. FORMOSA: Takow, 3 ♂, 3 ♀, vii.1907 (*H. Sauter*). CELEBES: Macassar, 5 ♂, 5 ♀. MOLUCCAS: Amboina, 4 ♀ (*W. Doherty*); Obi Is., 4 ♂, 4 ♀. NEW GUINEA: Argyll Bay, 1 ♂, 1 ♀, ix.1925 (*E. Ballard*); Pt. Moresby, 1 ♀; Murray I., 2 ♂, 1 ♀. BISMARCK ARCHIPELAGO: Long I., 1 ♂, x.1925 (*E. Ballard*). SOLOMON IS.: Guadalcanal, 4 ♂, 7 ♀, xi.1931 (*R. A. Lever*). NEW HEBRIDES: Malekula, 3 ♂, 3 ♀, Erromanga, 1 ♂ (*L. E. Cheesman*). QUEENSLAND: Yeppoon, 1 ♀; Lizzard I., 1 ♂, viii.1916 (*E. A. Briggs*); Magnetic I., 1 ♀ (*Scharff*). No label, 3 ♂, 2 ♀.

Type locality: Carteret I., Solomon Is.

LIST OF ETHIOPIAN, ORIENTAL AND AUSTRALASIAN SPECIES OF *Dysdercus* BOISDUVAL, WITH MORE IMPORTANT SYNONYMS.

- | | |
|--|---|
| <i>superstitiosus</i> (Fabricius, 1775). | <i>similis</i> sp. n. |
| syn. <i>volkeri</i> Schmidt, 1932. | <i>poecilus</i> (Herrich-Schäffer, 1844). |
| <i>nigrofasciatus</i> Stål. 1855. | <i>transversalis</i> Blöte, 1931. |
| <i>melanoderes</i> Karsch, 1892. | <i>concinnullus</i> Walker, 1872. |
| <i>flavidus</i> Signoret, 1861. | syn. <i>variegatus</i> Distant, 1902. |
| <i>ortus</i> Distant, 1909. | „ <i>incarnatus</i> Blöte, 1931. |
| <i>fasciatus</i> Signoret, 1861. | <i>festivus</i> Gerstaecker, 1892. |
| <i>cardinalis</i> Gerstaecker, 1873. | <i>cingulatus</i> (Fabricius, 1775). |
| <i>intermedius</i> Distant, 1902. | syn. <i>megalopygus</i> Breddin, 1909. |
| <i>orientalis</i> Schouteden, 1910. | <i>sidae</i> Montrouzier, 1861. |
| <i>pretiosus</i> Distant, 1902. | syn. <i>insularis</i> Stål, 1870. |
| <i>haemorrhoidalis</i> Signoret, 1858. | „ <i>biguttatus</i> (Walker, 1873.) |
| syn. <i>ugandanus</i> Schouteden, 1912. | „ <i>rubricutellatus</i> Breddin, 1901. |
| <i>koenigii</i> (Fabricius, 1775). | „ <i>remotus</i> Distant, 1914. |
| syn. <i>micropygus</i> Breddin, 1909. | <i>longiceps</i> Breddin, 1901. |
| <i>solenis</i> (Herrich-Schäffer, 1844). | <i>argillaceus</i> Bergroth, 1895. |
| syn. <i>ellanorae</i> Banks, 1909. | syn. <i>sordidulus</i> Breddin, 1901. |
| <i>evanescens</i> Distant, 1902. | <i>oceanicus</i> Boisduval, 1835. |
| <i>olivaceus</i> (Fabricius, 1798). | syn. <i>impictiventris</i> Stål, 1870. |
| syn. <i>luteolus</i> Breddin, 1909. | „ <i>albescens</i> Walker, 1872. |

- mesio stigma* Distant, 1888.
philippinus Herrich-Schäffer, 1853.
decussatus Boisduval, 1835.
 syn. *cruciatus* (Montrouzier, 1855).
 „ *fabricii* (Montrouzier, 1855).
 „ *crucifer* Stål, 1870.
 „ *simplex* (Walker, 1873).
 syn. *papuensis* Distant, 1888.
 „ *decorus* Breddin, 1901.
 „ *simon* Taeuber, 1927.
 „ *jacobsoni* Blöte, 1931.
 „ *sumatranus* Schmidt, 1932.
 „ *sauteri* Schmidt, 1932.

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A REVISION OF THE GENUS *BIDESSONOTUS* RÉGIMBART (COLEOPTERA : DYTISCIDAE)

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WITH TWELVE TEXT-FIGURES.

THIS genus was erected for a group of species previously indicated by Sharp (1882, *Biol. Centr.-Amer.*, 1 (ii) : 26) *adumbratus* (Clark), *pulicarius* (Aubé) and *caraïbus* (Chevrolat) and for other species newly described in the same place. The principal characters proposed were :—

A transverse impression on the head separating frons and clypeus ; the anterior edge of the frons unmargined ; the posteriorly parallel, anteriorly convergent and apically contiguous, strongly sulcate-impressed metacoxal lines ; and the evidently pentamerous tarsi of the anterior and intermediate legs.

The status of the group was reduced to that of a subgenus of *Bidessus* by Zimmermann (1917 (1919), *Arch. Naturg.* 83 (A) 12 : 144). It has again been raised to a full genus by Guignot (1939, *Bull. Soc. Sc. nat. Vacluse* 10 : 52) and *Hydroporus adumbratus* Clark (1863) named as genotype. Guignot unites with *Bidessonotus* two other groups, *Brachy-vatus* Zimmermann and a new subgenus, *Liodessus*, groups quite beyond the limits of the original definition of Régimbart and whose proper status will be dealt with in a forthcoming paper on the Aquatic Coleoptera of Mexico (excluding Lower California). It is only necessary here to say that I reject them as subgenera of *Bidessonotus*, which, on the characters selected by Régimbart, is undoubtedly to be accepted as a valid genus, with the following diagnostic characters added to the generic definition :—

Presence of a transverse cervical stria on the head immediately behind the eyes ; third segment of the pro- and mesotarsi not at all bilobate.

As thus restricted, the genus forms a very homogeneous aggregate and the external specific distinctions are neither obvious nor many. Secondary sexual characters, on the other hand, are many and obvious, comprising form, antennae, the basal segments of the anterior and intermediate tarsi, the intermediate tibiae, the intermediate femora, epipleurs, the apical ventrite and the course of the metacoxal lines. The aedeagus is built on a uniform plan, the lateral lobes more or less distinctly bilaterally asymmetrical ; the median lobe distinctly bilaterally asymmetrical, based on variations of an axe-shaped organ, the "shaft" being the basal portion of the median lobe, always with an angular projection near the base on the right side on the concave edge, the "blade" being a laterally flattened expansion of the apical portion of the lobe. The lateral lobes are, as in all *Bidessini*, tri-articulate, with the small third piece articulated interno-apically ; the proximal piece

of the left side may or may not possess a more or less distinct obtuse process on the inner side which presumably acts as a "locking device" on the basal projection of the median lobe.

The species designated as genotype by Guignot, *adumbratus* (Clark), was described on three specimens, two now in the British Museum and a third now in the Bishop Collection, Glasgow University Zoological Department. These specimens actually represent two distinct species, neither of which possesses the generic characters given above. The original error of identification is due to Sharp. In his Monograph on the DYTISCIDAE (1882, *Sci. Trans. R. Dublin Soc.* 2 (ii) : 786) he includes a transcript of Clark's description among the species not recognised by him. In his study of the Central American DYTISCIDAE (1882, *Biol. Centr.-Amer.* 1 (ii) : 26) he identifies the species as one from GUATEMALA : Paso Antonio, to which he later added specimens from MEXICO : Tabasco, PANAMA, and ISLAS PERLAS. The Guatemalan species is of the *caraiBUS-pulicarius* group and possesses the distinctive characters utilised by Régimbart in creating the genus ; I have redescribed it hereunder as *B. championi* nom. nov.

It is clear that *adumbratus* (Clark) is not the correct name for the genotype of *Bidessonotus*. According to Opinion 65 of the Rules of Nomenclature a genotype citation based on an erroneous identification is to be taken "as that species actually intended by the author." For the following reasons I think that the species actually intended by Guignot is unidentifiable and the provisions of Opinion 65 cannot, therefore, be fulfilled. In his paper Régimbart describes a species from "Mexique" under the name "*adumbratus* (Clark)." As I have shown above, this cannot be Clark's species and the description does not apply to *championi* mihi (*adumbratus* (Clark) Sharp *nec* Clark) nor to any other species known to me from Mexico. It would appear on this basis that *adumbratus* (Clark) Régimbart *nec* Clark *nec* Sharp is an unknown species and I propose to name it *régimbarti* nom. nov. Guignot does not give any diagnosis of his conception of the species and there is no means of knowing on what he has based his conception. *B. adumbratus* (Clark) Guignot *nec* Clark is therefore a *species incognitus* and cannot therefore be accepted as valid for purposes of a genotype citation.

Following on the elimination of Guignot's genotype citation, it is necessary to make a fresh designation of a genotype for *Bidessonotus*. As already stated, the genus was created principally for the three species *caraiBUS* (Chevrolat), *pulicarius* (Aubé) and *régimbarti* nom. nov. (*adumbratus* (Clark) Régimbart *nec* Clark *nec* Sharp), but other new species were described in the same paper. It would clearly be preferable to designate one of these three species as genotype, but, as I shall proceed to show, none of them can be accepted as satisfactory.

Hydroporus pulicarius Aubé (1838, *Spec. Col.* 6 : 495) was described from "États-Unis d'Amerique." It is said to be the *pulicarius* of Dejean's Catalogue (1836, *Cat. Coleopt.*, ed. 3 : 65), and Aubé also gives *Hydroporus lacustris* Say (1825) as a synonym. In his description of the insect Aubé states that the elytra "présentent une strie longitudinale assez fortement enfoncée tout le long de la suture . . .", a character not found in the species accepted as *pulicarius* by subsequent authors, nor in

lacustris (Say), although some specimens of what is accepted as that species may show a trace of a sutural stria. Both Sharp and Régimbart based their conceptions of *pulicarius* on females from Dejean's collection, the former on a specimen now in the British Museum, the latter on a specimen in Oberthur's collection. It is this conception of *pulicarius* which is accepted at the present time, but there seems reason to doubt if it is the true *pulicarius* of Aubé and in consequence it seems inadvisable to select this species as the genotype.

Hydroporus caraibus was described by Chevrolat from Cuba (1863, *Ann. Soc. ent. Fr.* (4) 3 : 199). The species was only known to Sharp and Régimbart by female specimens and, in the absence of males showing the definitive characters of the mesotibiae and aedeagus, its limits are uncertain. I have as yet seen no Cuban males which can properly be ascribed to this species and, in view of the close similarity of the various species, it also seems inadvisable to select this species as the genotype.

As I have shown above, the exact identity of *régimbarti* is not, at present, ascertainable and the species is, therefore, not available for genotypic designation.

In view of the foregoing facts a fresh, unambiguous, type designation is required and I here select *Bidessonotus obtusatus* Régimbart (1895), one of the new species described by Régimbart, as genotype.

Seven species are listed by Zimmermann (1920, *Junk, Col. Cat.* 71 : 61-62), with one full synonym. Two species were added by Blatchley (1919, *Bull. Amer. Mus. nat. Hist.* 41 : 310-311). The present revision shows a total of nineteen species and it has been considered advisable to prepare completely fresh descriptions according to a standard formula in order to make possible direct comparisons between the species. Of the nineteen species treated hereunder I have seen all but two of which the descriptions are copied from the original. The order in which the species are treated appears to follow a more or less natural arrangement so far as it has been possible to appreciate the relationships in a remarkable homogeneous aggregate.

Types of the new species are all in the British Museum (Natural History) with the exception of *B. fallax* sp. n., which is in the United States National Museum. I am indebted to Mr. L. L. Buchanan for the loan of that material.

Bidessonotus mobilis sp. n. (fig. 1).

Bidessus adumbratus (Clark) Sharp, 1887, *Biol. Centr.-Amer.* 1 (ii), Suppl. : 754 (partim.).

Oblongo-ovalis, parum elongatus ; capite fusco vel flavofusco ; pronoto flavo, ad basin inter plicas fusco-notato ; elytris fusco-flavis marginibus flavo-notatis ; subtus rufo-testaceus vel testaceo-flavus ; maris elytris sub-nitidis, subtiliter minus crebre punctulatis ; feminae opacis, haud iridescentibus, extus versus apices distincte obtuse dentatis ; tibiis pedorum intermediorum maris subtus fortiter curvatis.

Head fuscous or yellowish-fuscous, the anterior edge pale ; finely and not very closely punctulate between the eyes posteriorly, elsewhere very finely and very sparsely punctulate ; interstices of the punctulation shining, very obsoletely microreticulate. *Antennae* clear flavous, longer and more slender in the male. *Pronotum* flavous, narrowly infusate at the base between the plicae ; sides weakly rounded, distinctly margined ; basal plicae strongly impressed, slightly oblique and weakly curved, not exceeding half the length of

the pronotum from the base; almost impunctate, only a few rather fine shallow and obsolete punctures at the base between the plicae; shining, very obsoletely microreticulate in both sexes on the disc and between the plicae and the side margins near the base. *Elytra* yellowish-fuscous, darker in transverse basal, median and post-median bands, more obvious near the sides where the contrast is greater, but less obvious in the female; sides weakly rounded, widest about the middle, apically rounded attenuate in the male, obtusely rounded in the female; sub-nitid in the male, basally obsoletely, apically distinctly microreticulate, finely and evenly but not closely punctulate, the interstices two to three times the diameter of the punctures on the disc; opaque in the female, very finely and distinctly microreticulate, the punctures as in the male but apparently more obsolete; distinctly pubescent in both sexes; basal plicae slightly oblique, almost straight and barely longer than the pronotal plicae; near the apex the epipleurs in the female develop a distinct though small broadly obtuse tooth; epipleurs distinctly dilated in apical third. *Venter* reddish-testaceous or reddish-yellow, darker laterally on the metacoxae and the middle of the abdomen; metasternum impunctate, metacoxae and basal ventrites not very coarsely, irregularly and rather sparingly punctate; prosternal process hastate, shallowly longitudinally grooved through almost the whole length; apical ventrite of the male larger and more transverse than in the female, fairly strongly longitudinally rugose-punctate on each side. *Legs* flavous, the three basal segments of the anterior and intermediate tarsi of the male rather strongly incrassate; mesofemora of the male with a small acute tooth produced on the posterior edge of the ventral (tibial) furrow near the apex; intermediate tibiae of the male strongly curved beneath, of the female straight. *Aedeagus* with the terminal "blade" of the median lobe produced into a long, strong and recurved point, finely hooked at the tip; distal piece of the lateral lobes bilaterally asymmetrical at the apex, of the right side subtransversely truncate, of the left side angulate.

Size: 2.043–2.055 mm. long., 1.027–1.050 mm. lat.

Holotype ♂, MEXICO: Tabasco; San Juan Bautista (Hoege) (*Bidessus adumbratus* Clark, Sharp det.). Allotype ♀, same particulars as holotype.

This species, identified as *adumbratus* Clark by Sharp, is abundantly distinct from *championi* (*adumbratus* (Clark) Sharp (*partim*) *nec* Clark) by the less punctulate pronotum, the slightly less closely punctate elytra, the rugosities of the apical ventrite of the male, the distinctly curved intermediate tibiae of the male, the much more prominent sub-apical elytral tooth of the female and the dilated epipleurs in that sex and also by the form of the median lobe and distal pieces of the lateral lobes of the aedeagus. It may possibly prove to be the *adumbratus* of Régimbart (*régimbarti* mihi), but there are various discrepancies and the description given by Régimbart is inadequate for a definite determination which can only be decided by a study of authentic material.

The female allotype has the left antennae teratological, consisting of only eight segments. The first to sixth segments appear to be quite normal; the seventh and eighth appear to be quite normal penultimate and terminal tenth and eleventh segments; it thus appears that the normal seventh to ninth segments inclusive are completely missing.

Bidessonotus vicinus sp. n.

Ovalis, sat elongatus, testaceus; capite testaceo, antice vix impunctato, postice sat obsolete sparsim tenuiter punctulato, laevigato; pronoto testaceo, ad basin inter plicas anguste nigricante, in medio tenuiter sat sparsim, postice multo magis distincte et fortiore punctulato, laevigato; elytris sordide testaceis, lateraler dilutioribus, obsolete tenuiter punctulatis, fortiter microreticulatis, opacis, iridescentibus; epipleuribus postice distincte

explanatis, longitudinaliter canaliculatis, sub-apicaliter distincte denticulatis; subtus testaceus, metacoxis segmentisque basalibus abdominis lateraliter sat fortiter sparsim punctatis; processu prosternali sat distincte sed leviter longitudinaliter canaliculato. Mas ignotus.

Head testaceous, shining, anteriorly almost impunctate, posteriorly finely but rather obsoletely sparingly punctulate; transverse fronto-clypeal sulcus fairly deep at the sides, quite narrowly rather obsolete in the middle; transverse cervical stria very fine and rather obsolete. *Antennae* testaceous. *Pronotum* testaceous, narrowly blackish at the base between the plicae, shining, on the disc finely and rather sparsely punctulate, basally much more distinctly and strongly punctulate; the sides almost straight and sub-parallel in the basal half, thence rounded to the anterior angles, finely margined; basal plicae slightly oblique, almost straight, quite sharply but not strongly impressed, rather long, attaining almost two-thirds of the length of the pronotum from the base. *Elytra* ovate, sides very weakly rounded, widest about the middle, apically rounded attenuate, the sutural angle obtusely produced; finely, not very closely and rather obsoletely punctulate, the interstices about twice the diameter of the punctures on the disc; finely, very closely microreticulate, dull, iridescent; griseo-testaceous, paler laterally but with indistinct blackish spots at the shoulder, at the middle and behind the middle on the lateral declivity; basal plicae oblique, almost straight, sharply impressed, about as long as the pronotal plicae; epipleurs slightly but distinctly explanate posteriorly, longitudinally shallowly canaliculate, sub-apically distinctly acutely denticulate. *Venter* testaceous, rather shining, obsoletely microreticulate; prosternal process oblong, apically rounded, distinctly but shallowly longitudinally canaliculate; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) distinctly but shallowly impressed; metacoxae irregularly, rather obsoletely strongly punctate; laterally the basal abdominal segments more strongly and more closely punctate; apical ventrite rather strongly, fairly obsoletely but quite copiously punctulate. Male unknown.

Size: 1.762 mm. long., 0.915 mm. lat.

Holotype ♀, BRITISH HONDURAS: Punta Gorda, xii.1932 (J. J. White coll.). Paratype ♀, same particulars as holotype, but date i.vii.1933. (Head and pronotum missing.)

This little species cannot be satisfactorily placed in the absence of males, but it appears to belong near to *pulicarius* and *inconspicuus* by the dilated epipleurs and the strong anteapical denticulations. It is, however, evidently much smaller than either of these species and it seems probable that its nearest relatives may prove to be *mobilis* and *fallax*, which have the apex of the aedeagus developed into a strong pointed and upturned recurved spine. It is evidently smaller than the first-named species with less dilated epipleurs and is less copiously and rather less distinctly punctulate on the dorsum, particularly of the pronotum, than in that species.

Bidessonotus fallax sp. n. (fig. 2).

Bidessonotus caraihus Chevrolat, F. N. Young det. in coll.

Oblongo-ovalis, angustus, testaceus; capite testaceo, flavescente, in medio plus minusve infusato, antice tenuissime sat sparsim, postice paulo crebriore punctulato, laevigato; pronoto flavo-testaceo, postice inter plicas levissime vage infusato, antice tenuissime vix visibiliter, postice fortiore et distinctiore punctulato; elytris rufo-testaceis, lateraliter ad medium et ante apicaliter vage infusatis, tenuiter vix crebre distincte punctulatis, in mare sub-nitidis, in femina opacis, vix iridescentibus, epipleuribus feminae postice haud explanatis, sub-apicaliter acute dentatis; subtus testaceus, processu prosternali lanceolato, leviter longitudinaliter canaliculato; metacoxis segmentisque basalibus abdominis

lateraliter sat fortiter irregulariter punctatis; tibiis intermediis maris subtus fortiter curvato-emarginatis.

Head testaceous, yellowish, in the middle more or less vaguely infusate, anteriorly very finely and rather sparingly, posteriorly a little more closely punctulate, shining; the transverse fronto-clypeal sulcus quite distinct, narrowly interrupted in the middle; transverse cervical stria very distinct. *Antennae* testaceous, longer and more slender in the male than in the female. *Pronotum* flavo-testaceous, behind, between the basal plicae very slightly vaguely infusate; anteriorly very finely, scarcely visibly, posteriorly more strongly and distinctly punctulate; very obsoletely microreticulate in both sexes, slightly micant; basal plicae weakly sinuate, slightly oblique, quite strongly impressed at the base, attaining almost two-thirds of the length of the pronotum from the base; the sides weakly rounded, anteriorly slightly convergent, finely margined. *Elytra* reddish-testaceous, towards the sides at the middle and before the apex vaguely infusate, finely and evenly, scarcely closely distinctly punctulate, the interstices on the disc about twice the diameter of the punctures; in the male sub-nitid, rather obsoletely microreticulate; in the female dull, very finely distinctly microreticulate, scarcely iridescent; the elytral epipleurs in the female not at all explanate posteriorly, finely acutely denticulate before the apex; elongate-oval, the sides smoothly rounded, widest at about one-third of the length from the base, in the female more obtusely rounded at the apex than in the male; basal plicae almost straight, distinctly impressed, rather shorter than the pronotal plicae. *Venter* testaceous, the prosternal process lanceolate, bluntly pointed, weakly longitudinally canaliculate in the middle line; metasternum impunctate, the anteriorly convergent sulci (the anterior continuation of the coxal lines) moderately impressed; metacoxae and basal abdominal segments at the sides fairly strongly, not closely, irregularly punctate; apical ventrite in the male shallowly punctulate, faintly rugose longitudinally on either side of the middle line; in the female very finely sparingly punctulate, microreticulate, sub-nitid. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male barely at all incrassate, hardly wider than in the female; intermediate tibiae of the male strongly emarginate-curved beneath; mesofemora of the male not at all produced on the hind margin of the ventral (tibial) furrow near the apex. *Aedeagus* with the "blade" produced into a long, strong and apically hooked recurved point; lateral lobes with the distal piece bilaterally asymmetrical at the apex, of the right side obliquely truncate, of the left side transversely truncate, the ventral apical angle obliquely truncate.

Size: 1.445-1.663 mm. long., 0.708-0.767 mm. lat.

Holotype ♂, Cuba: Sta. Clara Province; Cayamas (*E. A. Schwarz* coll.) (*Bidessonotus caraiibus* Chevrolat, F. N. Young det.). Type No. 58270 in the United States National Museum. Allotype ♀, same particulars as holotype.

This little species must be closely related to *mobilis*, which it closely resembles in the form of the aedeagus. It is distinguishable from that species by the unarmed mesofemora of the male, the more slender lateral lobes of the aedeagus, the undilated epipleurs of the female, the much smaller and more acute sub-apical elytral denticulation of the female and the closer and more distinct elytral punctation. The more distinct elytral punctation of the female, the perfectly distinct sub-apical epipleural teeth, the shorter basal plicae of the elytra and the much more distinctly impressed microreticulation of the female readily serve to distinguish the species from the true *B. caraiibus* (Chevrolat).

Bidessonotus régimbarti nom. nov.

Bidessonotus adumbratus (Clark) Régimbart, 1895, *Ann. Soc. ent. Fr.* 64: 336, pl. 8, fig. 12, 12a. (*nec* Clark, *nec* Sharp).

Oblongo-ovalis, parum elongatus, subtus rufo-ferrugineus, coxis posterioribus saepe infuscatis, antennis pedibusque rufis, capite fusco, antice rufo, postice ferrugineo, rarissime omnino rufo, pronoto rufo, ad basin utrinque anguste nigro notato; elytris rufo-fuscis, basi, sutura anguste, macula laterali ad medium, altera post medium nigricantibus. Capite tenuiter postice punctulato, sulco transverso lato sat profundo, carina post-clypeali modice elevata; pronoto indistincte punctulato, plica obliqua, in elytris minus angulatum producta; elytris sat tenuiter dense punctatis, pubescentibus. Prosterni processu subtriangulari, elongato, profunde canaliculato, lineis coxalibus fortiter impressis, coxis sat fortiter haud dense punctatis.

♂ sat nitidus, sat elongatus, spatio inter lineas coxales latiore et excavato, tibiis intermediis fortiter curvatis.

♀ opaca, minor, elytris magis latis, ad apicem obtuse rotundatis.

Long. 1 $\frac{3}{4}$ –2 mill.

"Forme oblongue, couleur d'un roux ferrugineux, avec la tête fortement rembrunie au milieu, le pronotum étroitement marqué de noir de chaque côté de la base, les élytres d'un roux brun plus ou moins foncé, avec les taches pales et noirâtres laterales assez marquées. Ponctuation fine en arrière de la tête et le long de la base du pronotum, assez fine et dense sur les élytres, dont la pubescence est assez courte, grosse et espacée sur les hanches postérieures. Le sillon antefrontal est large et peu enfoncé, l'élevation, en arrière du clypeus, médiocre; le pli prothoracique est moins oblique, moins anguleusement prolongé sur les élytres. L'apophyse prosternale est presque triangulaire, avec une canelure large et profonde en forme de fossette; le sillon sutural de l'espace intermédiaire aux lignes coxales est profond.

"Dans les tabacs du Mexique, plusieurs exemplaires."

Bidessonotus longovalis (Blatchley) (fig. 3).

Bidessus longovalis Blatchley, 1919, *Bull. Amer. Mus. nat. Hist.* 41 : 810.

Elongato-ovalis, lateraliter leviter rotundatus, testaceus; capite antice flavo, postice infuscato, leviter sat sparsim punctulato, praecipue in medio, subobsolete reticulato; pronoto flavo, leviter sat crebre in medio punctulato, ad basin inter plicas magis distincte fortiterque punctato; plica obliqua utrinque sat fortiter impressa; elytris fusco-brunneis, lateraliter pallidioribus, tenuiter crebre punctulatis; subtus testaceus, metacoxis segmentisque basalibus abdominalis sat fortiter minus crebre punctatis; processu prosternali lanceolato, longitudinaliter obsolete sulcato; elytris maris rotundato-acuminatis; feminae obtuse rotundatis, dente obtuse sat distincte antepicali; tibiis intermediis maris subtus sat fortiter curvatis.

Head anteriorly flavous, posteriorly infusate, in the middle very finely and quite sparingly punctulate, elsewhere more sparingly and finely; interstices of the punctation sub-nitid, subobsoletely microreticulate. *Antennae* flavous. *Pronotum* flavous, slightly infusate basally between the plicae but not in the scutellar region; very finely punctulate, fairly densely so in the middle, near the base between the plicae more strongly and distinctly punctulate, the interstices here about equal to the diameter of the punctures; the basal plicae distinctly oblique except in the basal quarter where they are straight, the plicae therefore curved, quite strongly impressed, attaining slightly more than half the length of the pronotum from the base; the sides weakly but regularly rounded, finely and distinctly margined; on the disc obsoletely, between the plicae and the side margin subobsoletely finely microreticulate. *Elytra* brownish-fuscous, vaguely paler at the apex and narrowly testaceous at the sides; elongate, widest at middle, the sides rounded, apically rounded-attenuate in the male, obtusely rounded in the female, with, in that sex, a distinct obtuse ante-apical epipleural tooth; finely and densely punctulate, the interstices about equal to the diameter of the punctures on the disc; distinctly pubescent; in the male sub-nitid, very obsoletely microreticulate, in the female sub-nitid in the basal half, obsoletely microreticulate, dull in the apical half, distinctly microreticulate; basal plicae weakly sinuate at the base, weakly oblique, elongate, about one and one-half times as long as the pronotal plicae, shallow but sharply impressed; at the middle and behind the middle

two ill-defined blackish spots on the lateral declivity, but not attaining the side margin; elytral epipleurs distinctly dilated in apical third in the female, longitudinally sulcate before the tooth. *Venter* testaceous; prosternal process lanceolate, the apex rounded acute, narrowly and shallowly sulcate in the middle line; metasternum impunctate, metacoxae quite coarsely but not very closely punctate, basal abdominal ventrites at the sides coarsely, somewhat rugosely punctate; apical ventrite in the male larger and more transverse than in the female, quite finely and densely, not at all rugosely punctate; in the female finely and not very densely punctulate. *Legs* flavous, the two basal segments of the anterior and intermediate tarsi of the male slightly incrassate, the third barely incrassate; mesofemora in the male with a small obtuse tooth on the hind edge of the ventral (tibial) furrow near the apex; intermediate tibiae of the male moderately curved beneath, in the female straight. *Aedeagus* with the median lobe axe-shaped, the terminal "blade" straight, the "edge" obliquely truncate; lateral lobes with the distal piece terminally rounded, almost bilaterally symmetrical, internally at the apex with a small tuft of fine hairs and a comb-like structure.

Size: 2.271–2.440 mm. long., 1.118–1.189 mm. lat.

Redescribed from 2 ♂, 5 ♀ paratypes, UNITED STATES: Florida (*W. S. Blatchley* coll.). (B.M. 1935–440).

A fairly distinct species of larger size and having a more dense and distinct punctation.

Bidessonotus inconspicuus (LeConte) (fig. 4).

Hydroporus inconspicuus LeConte, 1855, *Proc. Acad. Sciô. Philad.* 7: 290, 294.

Oblongo-ovalis, sat elongatus; capite testaceo, tenuiter sat distincte punctulato; pronoto testaceo, tenuissime obsolete punctulato, ad basin inter plicas magis distincte et minus obsolete punctulato; elytris fusco-testaceis, marginibus anguste pallidioribus; subtus rufo-testaceus, metacoxis segmentisque basalibus abdominis lateraliter sat remote distincte punctatis; elytris maris subnitidis; feminae opacis, vage iridescentibus, extus versus apices distincte obtuse dentatis; tibiis intermediis maris subtus vix curvatis.

Head testaceous, finely but quite distinctly and moderately closely punctulate, the interstices about one and one-half times the diameter of the punctures in the middle, the interstices shining; transverse fronto-clypeal impression distinct in the male, subobsolete in the female. *Antennae* testaceous, slightly longer and more slender in the male than in the female. *Pronotum* testaceous, very finely, rather obsoletely and moderately closely punctulate except at the base between the plicae where the punctures are about twice the size of those on the disc, less obsolete and rather closer, the interstices being about equal to the diameter of the punctures; basal plicae slightly oblique except just at the base where they are straight, the plicae therefore slightly curved; not very strongly impressed and barely attaining half the length of the pronotum from the base; the sides weakly but regularly rounded, quite distinctly margined; surface shining. *Elytra* smoky-testaceous, the margins narrowly paler; elongate, widest at middle, the sides rounded, apically rounded-attenuate in the male, obtusely rounded in the female, with, in that sex, a very distinct pre-apical obtuse epipleural tooth; finely and quite densely punctulate, the interstices about equal to the diameter of the punctures on the disc; finely distinctly pubescent; the surface in the male shining in the basal half, dull, microreticulate in the apical half; in the female quite dull, very finely and closely microreticulate, weakly iridescent; basal plicae almost straight, rather shallow and weakly impressed, barely one-quarter longer than the pronotal plicae; at the middle and behind the middle two ill-defined blackish spots on the lateral declivity but not attaining the margin; elytral epipleurs distinctly dilated in apical third in the female, longitudinally sulcate before the tooth. *Venter* reddish-testaceous; prosternal process lanceolate, apically acutely rounded, longitudinally shallowly sulcate; metasternum impunctate, metacoxae and basal abdominal ventrites at the sides moderately remotely, quite distinctly and sharply punctate, the punctures fairly large and, on the

metacoxae, separated by about twice their diameters; apical ventrite in the male larger and more transverse than in the female, distinctly, densely but moderately finely punctulate, in the female basally somewhat sparsely aciculate punctulate, apically impunctate, shining. Legs flavo-testaceous; the two basal segments of the anterior and intermediate tarsi of the male distinctly, the third segment weakly, incrassate; intermediate tibiae of the male scarcely curved beneath, long and slender; in the female short and triangular; the mesofemora of the male with a small tooth on the lower hind margin of the ventral (tibial) furrow near the apex. Aedeagus with the median lobe axe-shaped, the terminal "blade" straight, the "edge" transversely truncate; the lateral lobes with the distal piece terminally rounded and weakly bilaterally asymmetrical, internally at the apex with a tuft of long hairs and a serrated comb-like structure; the dorsal edge of the proximal piece of the left lateral lobe rounded to the apex, not produced into an obtuse point at about half the length (cf. *pulicarius* Aubé).

Size: 2.034–2.271 mm. long., 1.017–1.118 mm. lat.

Redescribed from 1 ♂, 2 ♀ topotypes, UNITED STATES: Louisiana (Schaum) (B.M. 1848–69) (females *Bidessus pulicarius* Aubé, H. C. Fall det.). 1 ♀, "Am. Bor." (B.M. 1867–56) (*inconspicuus* LeConte (Schaum) det. Hamlet Clark) (*B. pulicarius* Aubé, Fall det.).

Other specimens examined: 1 ♂, 1 ♀, FLORIDA: Dunedin (*W. S. Blatchley* coll.); 1 ♀, FLORIDA: Royal Palm Park (*W. S. Blatchley* coll.); 1 ♀, INDIANA: Posey Co. (*W. S. Blatchley* coll.); 1 ♂, "AM. BOR." (ex Sharp coll.) (? *Bidessus pulicarius* Aubé var., Sharp det.).

This species was placed in synonymy with *B. pulicarius* (Aubé) by Sharp without comment (1880, *Sci. Trans. R. Dublin Soc.* 2 (ii): 364). The synonymy is accepted by Régimbart (*loc. cit.* 334) based on material received as *inconspicuus* from Sallé from Massachusetts and "United States." Zimmermann (1917 (1919), *Arch. Naturg.* 83 A (12): 145) appears to accept it without comment.

As I have mentioned above, the redescription is based upon three specimens from Louisiana in the British Museum received direct from Schaum in 1848 and also a fourth specimen from Hamlet Clark's collection received by him from Schaum. As LeConte received his material on which the species is based from Schaum there seems every reason to suppose that the British Museum specimens are topotypical and, loosely speaking, syntype material. The study of the genitalia of the material listed shows a constant difference from the series *pulicarius* and justifies the treatment of this as a distinct species.

Sharp's synonymy is probably based upon a single specimen labelled by him "*Hydroporus inconspicuus* Le Conte, Ind. auth., Florida," but this is quite certainly a female of *B. pulicarius*, of much smaller size, more sparingly punctured both dorsally and ventrally and with the basal pronotal plicae less oblique.

Bidessonotus pulicarius (Aubé) Sharp (fig. 5).

Hydroporus pulicarius Aubé, 1838, *Spec. Col.* 6: 494.

Bidessus pulicarius (Aubé) Sharp, 1882, *Sci. Trans. R. Dublin Soc.* 2 (ii): 364 (*partim.*).

Bidessonotus pulicarius (Aubé) Régimbart, 1895, *Ann. Soc. ent. Fr.* 64: 334.

Bidessus subsericeus Blatchley, 1919, *Bull. Amer. Mus. nat. Hist.* 41: 311. (*syn. nov.*)

Oblongo-ovalis, sat elongatus; capite testaceo, tenuissime vix distincte punctulato; pronoto testaceo vel sordide testaceo, tenuiter obsolete punctulato, ad basin inter plicas crassiore et minus obsolete punctulato; elytris sordide-testaceis vel brunneis, marginibus anguste dilutioribus; subtus testaceus, metacoxis segmentisque basalibus abdominis

lateraliter sat remote sat obsolete punctatis; elytris maris subnitidis, obsolete microreticulatis; feminae opacis, paulo iridescentibus, extus versus apices distincte obtuse dentatis; tibiis intermediis maris subtus vix curvatis.

Head testaceous, very finely and indistinctly, sparsely punctulate, the interstices two to two and a half times the diameter of the punctures in the middle, the interstices sub-obsolete microreticulate; transverse frontal impression distinct though shallow at the sides, obsolete in the middle in both sexes. *Antennae* testaceous, longer and more slender in the male than in the female. *Pronotum* smoky testaceous or more rarely testaceous, finely and obsoletely, rather sparsely punctulate, the interstices on the disc two and a half to three times the diameter of the punctures except at the base between the plicae where the punctures are about twice the size of those on the disc, less obsolete and separated by about their own diameter; basal plicae weakly oblique, slightly sinuate, rather weakly impressed and attaining quite half the length of the pronotum from the base; the sides weakly rounded, quite distinctly margined; the surface sub-nitid, obsoletely microreticulate. *Elytra* smoky testaceous or brownish, the margins narrowly paler; elongate, widest at middle, the sides rounded; apically rounded attenuate in the male, obtusely rounded in the female with, in that sex, a very distinct obtuse ante-apical epipleural tooth: finely and moderately densely punctulate, the interstices about one and a half times the diameter of the punctures on the disc; distinctly and finely pubescent; the surface in the male sub-nitid, obsoletely microreticulate; in the female quite dull, very finely and closely microreticulate, weakly iridescent; basal plicae weakly sinuate, shallowly impressed, about as long as the pronotal plicae; at the middle and behind the middle two ill-defined blackish spots on the lateral declivity, not quite attaining the margin; elytral epipleurs distinctly dilated in apical third in the female, longitudinally sulcate before the sub-apical tooth. *Venter* testaceous; prosternal process sub-lanceolate, apically sub-acute, longitudinally very obsoletely sulcate; metasternum impunctate, metacoxae and basal abdominal ventrites at the sides somewhat remotely and obsoletely coarsely punctate, the punctures on the metacoxae separated by about twice their diameters; apical ventrite in the male larger and more transverse than in the female, densely, rather rugosely punctured in the middle, the interstices reticulate. *Legs* testaceous, the basal segment of the anterior and intermediate tarsi of the male quite strongly incrassate, the second and third segments weakly so; intermediate tibiae of the male scarcely curved beneath, long and slender, of the female straight beneath, short, triangular; mesofemora without a tooth on the lower hind margin near the apex, at most slightly inflated and rounded here. *Aedeagus* with the median lobe axe-shaped, the terminal "blade" straight, the "edge" rounded; the lateral lobes with the distal piece transversely truncate at the apex, the ventral angle rectangular, the dorsal angle rounded, bilaterally very weakly asymmetrical, internally at the apex with a scanty tuft of long hairs and a serrated internal "comb"; the dorsal edge of the proximal piece of the left paramere produced into a broadly obtuse tooth at about the middle of the length (cf. *inconspicuus* LeConte).

Size: 1.932-2.034 mm. long., 0.881-1.017 mm. lat.

Redescribed from 1 ♂, 1 ♀, UNITED STATES: Indiana, Posey Co. (*W. S. Blatchley* coll.); 1 ♂, 1 ♀, UNITED STATES: Florida, Royal Palm Park (*W. S. Blatchley* coll.); 3 ♂, Florida, Crescent City (ex Horn).

Other specimens examined: 1 ♀ "Am. Bor." (*Hydroporus pulicarius* Aubé ex Mus. Dejean, Type mihi D.S.); 2 ♂, 5 ♀, UNITED STATES: Indiana, Posey Co.; 1 ♂, 2 ♀, Florida, Royal Palm Park; 9 specimens, UNITED STATES: Florida, Dunedin (*Bidessus subsericeus* Blatchley, cotypes); 1 ♀, Florida (*Hydroporus inconspicuus* LeConte, Ind. auth. = *pulicarius* Aubé mihi D.S.).

The identification of this species as the *pulicarius* of Aubé is due to Sharp. As already mentioned, Aubé described the species as possessing

a quite strongly impressed sutural stria and placed *lacustris* Say as a synonym. Neither Sharp nor Régimbart make any comment on the absence of a sutural stria in the species they accept as *pulicarius* of Aubé, which is the more remarkable as both these authors had before them material they evidently assumed to be the originals of Aubé's description. As far as can be ascertained, Zimmermann (1917, *loc. cit.* : 145) is the first author to comment on the discrepancies between the descriptions of Aubé and Régimbart, but he points out that Aubé, strangely, does not mention a sutural stria in the Latin diagnosis of the species in contradistinction to his usual practice elsewhere in the same volume ; from this fact it might be assumed that his Latin diagnosis and French descriptions were compiled from different species. The identity of the species is relatively fixed at present as being the species redescribed by Sharp and Régimbart, and accordingly it does not require any adjustment of nomenclature beyond the inclusion of Sharp as part author fixing the identity.

As already stated, the species is slightly but consistently distinct from *inconspicuus* (LeConte), the size averaging distinctly smaller, the males attaining only the size of the females of that species ; the punctuation is slightly sparser in both sexes ; the ante-apical epipleural tooth is usually more acute and the aedeagal differences confirm these external slight morphological divergences. The species is said by Régimbart to have a dimorphic form of the female of male-like appearance but with the intermediate tibiae straight beneath. I have seen no specimens of this form in the available material, but I suspect them to be the females of the related species, *B. longovalis* (Blatchley), redescribed above.

Bidessonotus caraïbus (Chevrolat).

Hydroporus caraïbus Chevrolat, 1868, *Ann. Soc. ent. Fr.* (4) 3 : 199.

Bidessus caraïbus (Chevrolat) Sharp, 1882, *Sci. Trans. R. Dublin Soc.* 2 (ii) : 364. Régimbart, 1895, *Ann. Soc. ent. Fr.* 64 : 335.

Oblongo-ovatus, elongatus ; capite testaceo, persubtilissime sparsim punctulato ; pronoto testaceo, tenuiter sat sparsim punctulato, ad basin inter plicas crassiore punctato ; elytris sordide testaceis, marginibus dilutioribus ; subtus testaceus, metacoxis obsolete sat remote punctatis, segmentis basalibus abdominis lateraliter sat fortiter irregulariter punctatis ; elytris feminae sat opacis, tenuiter sat distincte, praecipue postice, microreticulatis, extus versus apices tenuiter vix distincte acute dentatis. (Maris, tibiis intermediis curvatis ; elytris persubtilissime vix visibiliter reticulatis.)

Head testaceous, very finely and sparingly punctulate, the interstices (in the female) from two to four times the diameter of the punctures in the middle, shining, very obsoletely microreticulate ; transverse fronto-clypeal sulcus very shallow at the sides, almost obsolete in the middle. *Antennae* flavo-testaceous, the segments fairly stout. *Pronotum* testaceous, the disc finely and quite sparingly punctulate, the interstices about three times the diameter of the punctures, at the base more coarsely but not much more densely punctate ; basal plicae weakly oblique, weakly sinuate, sharply impressed, fairly long, attaining almost two-thirds of the length of the pronotum from the base ; the sides weakly rounded, finely margined ; surface shining, very obsoletely microreticulate on the disc, less obsoletely between the plicae and the side margins. *Elytra* smoky-testaceous, paler laterally, with a faint median and post-median blackish spot on the lateral declivity ; sub-nitid, particularly anteriorly where the reticulation is sub-obsolete, rather dull posteriorly where the reticulation is distinct ; rather finely and not very closely but regularly punctulate, the interstices on the disc about twice the diameter of the punctures ; basal plicae almost straight, moderately strongly impressed,

about as long as the pronotal plicae; distinctly and finely pubescent; ovate, the sides rounded, widest at middle, apically rounded attenuate; a very weak, barely visible acute ante-apical tooth on the epipleurs present in the female, the epipleurs not the least widened and not at all longitudinally sulcate in the posterior third. *Venter* testaceous; prosternal process lanceolate, the apex rounded-acute; longitudinally shallowly sulcate in the middle; metasternum impunctate; metacoxae rather obsoletely and rather remotely punctate; basal abdominal ventrites quite strongly but rather irregularly coarsely punctate at the base; moderately shining, microreticulate. *Legs*: mesotibiae of the female straight beneath (of the male curved beneath, according to Régimbart).

Size: 2.034–2.135 mm. long., 0.983–1.017 mm. lat. (♀).

Redescribed from 3 ♀, "CUBA" (2 labelled "*Hydroporus caraibus* Chev., Ind. typ., Type mihi D.S.") (1 labelled "*H. (exilis* Mus.Berol.)" ex Hamlet Clark (B. M. 67–56)).

Chevrolat does not specify the amount of material studied, nor does he describe the sexual differences. Sharp had only two female specimens, now in the British Museum (Natural History), in his collection. Régimbart states that he knew only two specimens, both males, from Wehnke's collection, which he asserts served Sharp for his description. I have not seen the male of this species and extract the relevant parts of the redescription above from that of Régimbart. In the absence of males for dissection it is not possible to place this species with any degree of confidence. It is undoubtedly distinct and appears to be not closely related to the two species treated immediately above, but closer to *championi* sp. n. described below by the undilated epipleurs immediately preceding the ante-apical tooth. It is quite distinct from another Cuban species (*fallax* sp. n.) which has been mistaken for it but which has been found to be new and more closely related to *mobilis* sp. n.

Bidessus championi sp. n. (fig. 6).

Bidessus adumbratus (Clark) Sharp, 1882, *Biol. Centr.-Amer.* 1 (ii): 25 (*partim.*) nec Clark.

Oblongo-ovalis, elongatus; capite sordide testaceo, antice sparse, postice sat crebre tenuiter punctulato, obsoletissime microreticulato; pronoto testaceo, ad basin inter plicas sat late infuscato; sat sparsim tenuiter punctulato, ad basin inter plicas crassiore punctato; elytris sordide testaceis vel brunneis, lateraliter dilutioribus; subtus testaceus, metacoxis segmentisque basalibus abdominis lateraliter sat fortiter irregulariter punctatis; elytris maris subnitidis, subobsolete reticulatis, feminae opacis, distincte iridescentibus, microreticulatis, extus versus apices tenuiter vix distincte acute dentatis; tibiis intermediis maris parum curvatis.

Head rather smoky testaceous, particularly laterally; anteriorly quite sparsely, posteriorly quite closely finely punctulate; transverse fronto-clypeal sulcus quite strongly impressed in both sexes. *Antennae* flavous, slightly longer and more slender in the male than in the female. *Pronotum* testaceous, at the base between the plicae quite widely infuscate, on the disc finely and somewhat sparingly punctulate, the interstices about three times the diameter of the punctures, at the base between the plicae slightly more closely and coarsely, the interstices about one and a half times to twice the diameter of the punctures; basal plicae distinctly oblique and slightly curved, strongly impressed and quite short, barely attaining half the length of the pronotum from the base; sides weakly rounded, distinctly margined; surface shining in the male, obsoletely reticulate and slightly less shining in the female. *Elytra* smoky testaceous or brownish, the sides paler with faint blackish median and post-median spots on the lateral declivity; in the male shining anteriorly with an obsolete reticulation, dull, distinctly microreticulate posteriorly; in the

female dull, distinctly iridescent, very finely microreticulate; the sides rounded, widest at middle, apically rounded-attenuate in both sexes, the sutural angle very slightly acuminate; finely and distinctly, moderately closely punctulate, the interstices about one or one and a half times the diameter of the punctures; the epipleurs of the female not dilated in apical third, near the apex produced into a very small acute tooth; basal plica very weakly curved, almost straight, quite strongly impressed, about as long as the pronotal plicae. *Venter* testaceous, prosternal process sub-hastate, apically rounded attenuate, longitudinally shallowly and rather obsoletely sulcate; metasternum impunctate; metacoxae and basal abdominal ventrites laterally quite strongly, not very closely and rather irregularly punctate; apical ventrite of the male larger and more transverse than of the female, moderately finely but somewhat obsoletely and sparsely punctulate, of the female finely and fairly distinctly and slightly more densely punctulate. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male quite distinctly incrassate; mesofemora of the male with a strong, rather obtuse tooth on the posterior edge of the ventral (tibial) furrow near the apex; intermediate tibiae of the male not very strongly arcuate, somewhat bisinuate beneath; of the female straight beneath. *Aedeagus* with the median lobe axe-shaped, the "blade" straight, the "edge" obliquely truncate, terminally acutely pointed; lateral lobes with the distal piece terminally bilaterally weakly asymmetrical, the ventro-terminal angle almost rectangular, the dorso-terminal angle widely rounded; internally at the apex with a fringe of moderately short hairs and a serrated pseudo-lacinal edge; the medial lobe twisted towards the left.

Size : 2.135-2.237 mm. long., 1.084-1.118 mm. lat.

Holotype ♂, GUATEMALA : Paso Antonio, 400 feet (Champion) (*Bidessus adumbratus* Clark, Sharp det.). Paratypes : 1 ♂, 5 ♀, same particulars as holotype.

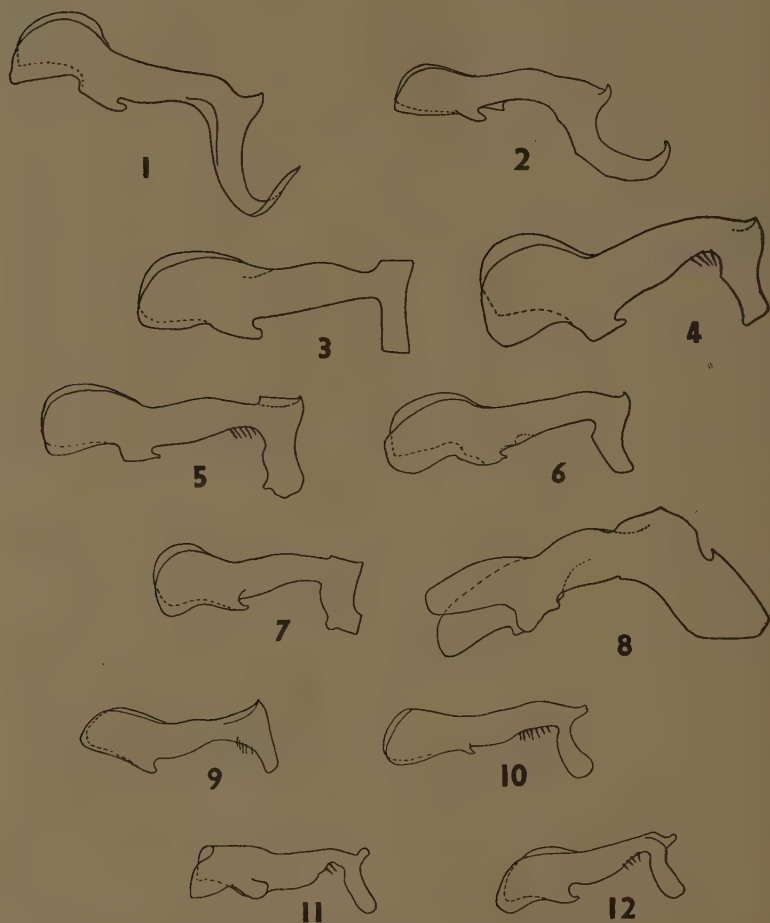
As already explained, the *adumbratus* of Clark does not belong to *Bidessonotus* and the species presumed by Sharp to be the same proved to be composite. The fact that Sharp had a suspicion that his identification was erroneous is suggested by a query mark preceding his identification in six of the seven specimens. The species is fairly similar to *caraihus* (Chevrolat) and also to the following species. It is rather larger and broader than the former, the head and middle of the pronotum near the base are infusate, the elytra of the female are duller, distinctly iridescent, the punctation more distinct.

Bidessonotus mexicanus Régimbart.

Bidessonotus mexicanus Régimbart, 1895, *Ann. Soc. ent. Fr.* 64 : 333, pl. 8, figs. 10, 11.

Oblongo-ovalis, sat elongatus; capite flavo-testaceo, antice sparsim tenuissime, postice magis crebre tenuiter punctulato; pronoto flavo-testaceo, ad basin utrinque inter plicas anguste infusato, tenuiter sat sparsim punctulato, ad basin inter plicas magis crebre fortiterque punctulato; elytris pallide fusco-testaceis, marginibus dilutioribus, tenuiter sat crebre punctulatis; feminae microreticulatis, extus versus apices tenuiter acute denticulatis; subtus testaceus, segmentis abdominis pectoreque in medio dilutioribus; metacoxis segmentisque basalibus abdominis lateraliter sat fortiter punctatis (maris tibiis intermediis parum curvatis).

Head flavo-testaceous, anteriorly very finely and sparsely, posteriorly more closely and finely punctulate; transverse fronto-clypeal sulcus deep, except in the middle (female) where it is quite shallow; surface shining. *Antennae* flavous. *Pronotum* flavo-testaceous, at the base between the plicae on each side narrowly infusate; finely and quite sparingly punctulate except at the base between the plicae where the punctures are more dense and stronger; basal plicae distinctly oblique, quite strongly impressed, not exceeding half the



FIGS. 1-12—AEDEAGUS, LEFT LATERAL ASPECT.

- 1.—*Bidessonotus mobilis* sp. n., holotype.
- 2.—*B. fallax* sp. n., holotype.
- 3.—*B. longovalis* (Blatch.), cotype.
- 4.—*B. inconspicuus* (LeConte), topotype.
- 5.—*B. pulicarius* (Aubé) Sharp.
- 6.—*B. championi* sp. n., cotype.
- 7.—*B. obtusatus* Rég.
- 8.—*B. browneanus* sp. n., holotype.
- 9.—*B. peregrinus* sp. n., holotype.
- 10.—*B. sobrinus* sp. n., holotype.
- 11.—*B. morosus* sp. n., cotype.
- 12.—*B. tibialis* Rég.

length of the pronotum from the base ; the sides weakly rounded, finely but distinctly margined ; surface shining on the disc, obsoletely microreticulate between the basal plicae and the margin. *Elytra* pale fusco-testaceous, at the shoulder, at the middle and behind the middle an ill-defined blackish spot on the lateral declivity, the sides paler ; finely and quite closely punctulate, the interstices about one and a quarter times the diameter of the punctures, microreticulate, more obsoletely so in the anterior half but quite distinctly, dull, iridescent ; the sides rounded, widest at middle, apically rounded, the sutural angle minutely acuminate ; at the sides near the apex in the female finely obtusely toothed at the epipleurs ; the epipleurs fairly broad at the level of the three basal ventrites but not dilated or longitudinally sulcate ; basal plicae oblique, straight, quite strongly impressed, barely longer than the pronotal plicae. *Venter* testaceous, the middle of the abdominal ventrites and the coxal lamellae paler ; prosternal process subparallel, the apex rounded, longitudinally quite strongly sulcate in the middle ; metasternum impunctate ; metacoxae quite strongly but not very densely punctate, basal abdominal ventrites at the sides quite strongly but irregularly and rather sparingly punctate ; apical ventrite moderately densely and finely but quite distinctly punctulate, the interstices about one and a quarter times the diameter of the punctures, microreticulate. *Legs* testaceous (intermediate tibiae of the male not very strongly curved).

* Size : 2.034 mm. long., 1.051 mm. lat.

Redescribed from 1 ♀, MEXICO : Teri ; Tepic (B.M. 1910-150).

The male of this species is known to me only by description and the above specimen is identified by description only, so I am not certain that the identification is correct. The species is, however, distinct from those known to me and answers fairly satisfactorily to Régimbart's description, inadequate though that is for modern identification. The species seems to be close to *championi*, slightly smaller and less elongate, less dull in the female with the elytral denticulation more obtuse, the epipleurs broader, the punctation about the same.

Bidessonotus obtusatus Régimbart (fig. 7).

Bidessonotus obtusatus Régimbart, 1895, *Ann. Soc. ent. Fr.* 64 : 336.

Bidessus pulicarius Aubé, Sharp, 1882, *Sci. Trans. R. Dublin Soc.* 2 (ii) : 364, *partim*.

Ovalis, elongatus, sat latus ; capite testaceo vel fusco-testaceo, antice tenuissime sat sparse, postice magis dense tenuiter punctulato, obsolete microreticulato ; pronoto testaceo, tenuiter obsolete punctulato, versus basin inter plicas obsolete sed fortiore punctulato ; elytris ovatis, fuscis, post basin sat late, post medium lateraliter et apicaliter pallidioribus ; tenuiter sat crebre et sat obsolete punctulatis, maris subopacis, distincte tenuiter microreticulatis, feminae opacis, iridescentibus, pertenuissime microreticulatis, epipleuribus apicaliter leviter explanatis, haud denticulatis ; subtus testaceus vel fusco-testaceus, pectore segmentisque basalibus abdominis in medio pallidioribus ; metacoxis segmentisque basalibus abdominis lateraliter distincte crebreque punctatis ; tibiis intermediis maris subtus curvatis ; processu prosternali fere plano, haud longitudinaliter canaliculato.

Head testaceous or fusco-testaceous, anteriorly very finely and quite sparingly, posteriorly finely and more densely punctulate, obsoletely microreticulate ; transverse fronto-clypeal sulcus deep at the sides, widely obsolete in the middle ; transverse cervical stria distinct but very fine. *Antennae* testaceous, in the male slightly longer than in the female. *Pronotum* testaceous, finely and rather obsoletely punctulate on the disc, towards the base, between the plicae, more strongly and less obsoletely punctulate ; basal plicae oblique, slightly curved, strongly but shallowly, almost foveolate-impressed, barely attaining half the length of the pronotum from the base ; the sides rounded apically, almost straight and sub-parallel in the basal half, finely but distinctly margined ; surface dull, discally obsoletely, at the sides distinctly microreticulate. *Elytra* fuscous, widely at the base from the margin but not extending inwards of the basal plica, laterally behind the middle and

apically testaceous; finely but rather obsoletely and fairly densely punctulate, the interstices on the disc about one and a quarter times the diameter of the punctures; rather dull in the male, distinctly finely microreticulate, quite dull and iridescent in the female, excessively finely microreticulate; the epipleurs in the female weakly explanate posteriorly, apices weakly longitudinally sulcate, without trace of a sub-apical tooth; oval, the sides rounded, widest at middle, apically rounded attenuate, not more obtusely in the female than in the male, the sutural angle barely acuminate; basal plicae weakly sinuate, faintly oblique, rather shallowly impressed and about one and a third times the length of the pronotal plicae. *Venter* fusco-testaceous, metasternum and basal abdominal ventrites paler in the middle; prosternal process quite broadly lanceolate, the apex rounded, almost flat, the sides not margined and not at all medianly longitudinally sulcate, dull, microreticulate; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) moderately sharply impressed; metacoxae and basal abdominal segments laterally closely and distinctly punctate; apical ventrite of the male fairly closely and rather finely, not at all rugosely punctulate, of the female slightly less closely punctulate, shallowly excavated at the apex. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male distinctly incrassate; meso-femora of the male with a very obtuse, barely produced tooth on the posterior edge of the ventral (tibial) furrow near the apex; mesotibiae of the male distinctly curved beneath, weakly sinuate. *Aedeagus* with the median lobe axe-shaped, the "blade" straight, the "edge" obtusely asymmetrically angulate; parameres bilaterally asymmetrical, the left with the distal piece terminally obliquely truncate, the right with the distal piece terminally weakly emarginate, broader than the left, apically with a fringe of long hairs and a very short, finely serrated "lacinial" edge.

Size: 1.863-2.102 mm. long., 1.010-1.169 mm. lat.

Redescribed from 1 ♂, 1 ♀, BRAZIL: Santa Rita (*Sahlberg* coll. "323"), ex. coll. Sharp. 4 ♂, 3 ♀, BOLIVIA: Santa Ana, 14.viii.1937 (*H. E. Hinton* coll.).

This species was described on two females, one from BRAZIL: Boa Sorta (*Sahlberg*) which *Régimbart* asserts is an *ex typis* of *pulicarius* Sharp (although Sharp only mentions two South American specimens of that species, both from Santa Rita) and one from Central Paraguay (*P. Germain*). The male does not appear to have been hitherto described. The species is quite distinct but appears to be fairly closely related to *championi*, although shorter and more distinctly microreticulate in both sexes. I have also seen one male, lacking thoracic sterna and abdomen, and two females from BRAZIL: Matto Grosso; Corumba, determined by *Knisch*.

Bidessonotus truncatus sp. n.

Ovalis, sat latus, minus elongatus, testaceus; capite flavo-testaceo, tenuissime punctulato, laevigato, sulco fronto-clypeali lateraliter sat profunde, in medio sat late obsoleto; pronoto flavo-testaceo, ad basin inter plicas anguste nigricante, in medio tenuissime sat sparsim, versus basin fortiore et magis distincte punctulato; elytris griseo-testaceis lateraliter vix pallidioribus; tenuiter sat crebre sat obsolete punctulatis, tenuissime microreticulatis, iridescentibus; epipleuribus postice sat explanatis, tenuiter longitudinaliter canaliculatis, haud dentatis; postice sub-truncatis, obtusis; subtus testaceus, metacoxis segmentisque basalibus abdominis sat obsolete sparsim fortiter punctatis. Mas ignotus.

Head flavo-testaceous, very finely punctulate, more sparingly in the middle, shining; transverse fronto-clypeal sulcus quite deep at the sides, widely obsolete in the middle; transverse cervical stria distinct. *Antennae* flavo-testaceous. *Pronotum* flavo-testaceous, narrowly blackish at the base between the plicae; very finely and rather sparingly punct-

tulate on the disc, more strongly and more distinctly near the base; shining, the sides weakly rounded, quite strongly margined; basal plicae oblique, curved, sharply and rather widely impressed, attaining just half the length of the pronotum from the base. *Elytra* greyish-testaceous, scarcely visibly paler at the sides; finely, fairly closely and rather obsoletely punctulate, the interstices on the disc hardly more than one and a quarter times the diameter of the punctures; very finely microreticulate, dull, iridescent; the epipleurs moderately explanate posteriorly, finely and distinctly longitudinally canaliculate at the apex, not at all dentate before the apex; oval, rather wide, widest at middle, apically almost truncate, very obtuse; basal plicae almost straight, quite sharply impressed, about one and a half times the length of the pronotal plicae. *Venter* testaceous, finely obsoletely microreticulate; the prosternal process elongate, lanceolate, basally shallowly longitudinally canaliculate; metasternum impunctate; metacoxae and basal abdominal segments at the sides rather obsoletely, sparingly strongly punctate; apical ventrite very finely, fairly closely and regularly punctulate. *Legs* testaceous.

Size: 2.118 mm. long., 1.084 mm. lat.

Holotype ♀, BRAZIL: Rio Grande do Sul; Porto Alegre, ix.1941 (R. Kleerekoper coll.). Unique.

This unique specimen appears to be close to *B. obtusatus* Régimbart, but is distinct by the shallowly canaliculate, not flat prosternal process, by the markedly obtuse, almost truncate apices of the elytra and the obsolete, rather sparing punctation of the metacoxae and sides of the basal abdominal segments. I have very little hesitation in naming this as a distinct species on this unique specimen and in spite of the absence of the male.

Bidessonotus browneanus sp. n. (fig. 8).

Elongato-ovalis, sat latus; capite testaceo, laevigato, antice pertenuissime sat sparsim, postice tenuiter in medio paulo crebriore punctulato; pronoto testaceo, ad basin inter plicas anguste infuscato, tenuiter sat sparsim punctulato, versus basin fortiore et crebriore punctato, laevigato, extus obsolete microreticulato; elytris fusco-testaceis maculis post humerale, post mediale et apicale pallidioribus, tenuiter minus crebre punctulatis, antice obsolete, postice distincte microreticulatis, femina sub-iridescente; subtus testaceus, lateraliter sat infuscatus, metacoxis segmentisque basalibus abdominis lateraliter distincte punctatis; tibiis intermediis maris subtus fortiter bisinuatis, curvatis; feminae subtus rectis, triangularibus; elytris feminae postice lateraliter vel distincte obtuse dentatis vel muticis.

Head testaceous, shining, anteriorly extremely finely and quite sparingly, posteriorly in the middle finely and slightly more densely punctulate; anteriorly finely microreticulate; the transverse fronto-clypeal sulcus shallow, obsolete in the middle in both sexes; transverse cervical stria distinct. *Antennae* not particularly long and not visibly sexually dimorphic. *Pronotum* testaceous, at the base between the plicae narrowly infuscate; finely and rather sparingly punctulate on the disc, towards the base more strongly and more densely punctate; shining, between the plicae and the side margins obsoletely microreticulate in both sexes; basal plicae oblique, curved, strongly impressed, not attaining much more than half the length of the pronotum from the base; the sides very weakly rounded, almost straight in the basal half, finely but distinctly margined. *Elytra* fusco-testaceous, at the sides behind the shoulder, behind the middle and at the apex vaguely paler, the pale spots united along the margin and separated by a humeral, median and post-median ill-defined black spot on the lateral declivity; regularly, finely but not very closely punctulate, the interstices one and a half to twice the diameter of the punctures on the disc; oval, the sides rounded, widest at middle, in the male apically rounded-attenuate, in the female widely rounded, the sutural angle minutely divaricate, before the apex on each side a small but distinct obtuse tooth or quite without an ante-apical tooth;

the epipleurs not at all explanate in front of the denticle; anteriorly obsoletely microreticulate, posteriorly distinctly but finely microreticulate in both sexes, the female more finely and sub-iridescent; basal plicae shallowly but distinctly impressed, very slightly sinuate, long, about one and a quarter times the length of the pronotal plicae. *Venter* testaceous, the sides of the metacoxae and basal abdominal segments rather infuscate or castaneous; prosternal process lanceolate, the apex sharply rounded, longitudinally shallowly but distinctly sulcate; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the metacoxal lines) very shallow and rather obsolete; metacoxae and basal abdominal segments at the sides irregularly and not very closely strongly punctate, finely microreticulate; apical ventrite in the male larger and more transverse than in the female, regularly convex, finely and regularly punctulate, medially sub-obsoletely, laterally distinctly microreticulate; in the female with the apical third longitudinally concave, the anterior edge of the concavity forming an obsoletely tectiform transverse ridge, much more finely and sparingly punctulate than in the male, shining. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male distinctly incrassate; intermediate femora of the male with the posterior edge of the ventral (tibial) furrow produced into a distinct very obtuse tooth near the apex; intermediate tibiae of the male distinctly and quite strongly bisinuate beneath, curved, in the female straight beneath, triangular. *Aedeagus* with the median lobe axe-shaped, the "blade" large, almost straight, the edge strongly produced in the middle, the angle in the middle about rectangular; distal pieces of the lateral lobes strongly bilaterally asymmetrical, the right terminally sub-triangular, the ventral apical angle acute, the dorsal apical angle produced into a short tooth, of the left apically weakly sinuate, almost straight.

Size: 2.00-2.083 mm. long., 1.017-1.085 mm. lat.

Holotype ♂, JAMAICA, B.W.I.: Gayle, "Slow stream," 30.vii.1929 (*F. Balfour-Browne* coll.). Allotype ♀, same particulars as holotype. Paratypes: 2 ♀, same particulars as holotype; 1 ♀, JAMAICA, B.W.I.: Moneague, 31.vii.1929 (*F. Balfour-Browne* coll.); 1 ♀, JAMAICA (without further particulars), 1858; (*J. Gray* coll.).

The aedeagus of this species will serve adequately to distinguish the male from all the other species described in the present paper; the much larger "blade" of the median lobe with the strongly produced "edge" and the very distinct form of the parameres and their strong bilateral asymmetry separate it from all the males I have seen. It is also remarkable in that the female is dimorphic as to the presence or absence of the ante-apical tooth of the elytra, the only instance yet known to me in this genus of such dimorphism.

Bidessonotus nepotinus sp. n.

Elongato-ovalis, testaceus; capite testaceo, antice tenuissime postice tenuiter obsoletely punctulato; obsoletely microreticulato; pronoto tenuiter sat irregulariter punctulato, sat obsoletely microreticulato, iridescente; elytris testaceis vage transversim fusco-tri-maculatis, tenuiter crebre punctulatis, opacis, iridescentibus microreticulatis; versus apices extus muticis. Mas ignotus.

Head testaceous, anteriorly very finely, posteriorly finely obsoletely punctulate, obsoletely microreticulate; transverse fronto-clypeal sulcus shallow, widely obsoletely in the middle; transverse cervical stria very fine, rather obsoletely and indistinct. *Antennae* flavo-testaceous, moderately long. *Pronotum* entirely testaceous, finely and rather irregularly punctulate, a few punctures at the base on each side just within the plicae rather larger and more distinct; obsoletely microreticulate, rather shining, somewhat iridescent; basal plicae distinctly curved, slightly oblique, quite strongly and widely impressed, attaining just half of the length of the pronotum from the base; the sides rounded, distinctly but finely margined. *Elytra* testaceous, vaguely infuscate in three transverse bands, one at the

base widest in the middle and tapering towards each side, one in the middle not quite attaining the margins and a third post-medianly both anteriorly and posteriorly sinuate, none of the bands very distinct or sharply delimited; finely and rather closely punctulate, the interstices on the disc not much more than the diameter of the punctures; distinctly, finely microreticulate, dull, iridescent; ovate, the sides rounded, widest at middle; the epipleurs not dilated and not at all produced into a small tooth shortly before the apex; basal plicae slightly oblique, weakly sinuate, rather shallow but distinctly impressed, about one and a quarter times the length of the pronotal plicae. *Venter* testaceous, finely and sub-obsolete microreticulate; prosternal process lanceolate, the apex rounded-acute, broadly transversely tectiform or rounded, without a trace or with at most a very fine median longitudinal sulcus; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) shallow but distinct; metacoxae and basal abdominal segments at the sides irregularly and rather shallowly punctate; apical ventrite fairly densely finely obsolete punctulate. *Legs* testaceous. Male unknown.

Size: 2.152-2.169 mm. long., 1.050-1.085 mm. lat.

Holotype ♀, TRINIDAD, B.W.I.: St. Augustine, 29.xii.1923 (C. L. Withycombe coll.). Paratype, 1 ♀, same particulars as holotype.

An apparently quite distinct species with the elytral pattern more visible than in any other species I have seen. I have placed it in the group of species gravitating around *championi* with considerable hesitation because of the absence of the male for the definite characters for comparison. It appears to be near *obtusatus* in many characters, however, and it is not impossible that further material may show it to be a local form of that species.

Bidessonotus melanocephalus Régimbart.

Bidessonotus melanocephalus Régimbart, 1895, *Ann. Soc. ent. Fr.* 64 : 332.

Oblongo-ovalis, sat elongatus, infra fuscus, plus minus in abdomine ferrugato, antennis pedibusque rufis, capite nigro, ore vix ferrugato; pronoto rufo, ad basin plus minus nigricante, elytris fuscis, ad latera indistincte ferrugineo tinctis. Corpore persubtilissime reticulato, capite tenuissime et indistincte punctulato, sulco transverso postclypeali fortiter impresso, carina transversa postclypeali elevata et valde conspicua; pronoto in disco tenuiter parum distincte punctulato, secundum basin sat fortiter punctato, lateribus arcuatis et cum elytris angulum praebentibus, plica utrinque profunda, in elytris angulatim continuata, angulis posterioribus rectis; elytris sat fortiter dense punctatis, pubescentibus. Prosterni processu leviter canaliculato, subtriangulari, coxis posterioribus in medio grosse fortiter punctatis, lineas coxalibus profunde canaliculatis. ♂. Sat nitidis elytris elongatis, spatio inter lineas coxales latiore, multo magis excavato, tibiis intermediis fortiter curvatis. ♀. Opaca, fortius reticulata, elytris tenuis punctatis, minus elongatis, postice multo magis obtusis.

Long. 2-2½ mm.

“Cette espèce est la plus foncée en couleur. Sa forme est oblongue-ovale, assez allongée, avec l'angle thoraco-élytrale bien accusé, sa couleur est un brun-noir en dessous, à reflets ferrugineux sur l'abdomen et sur le milieu de la poitrine, noire sur la tête, qui est à peine ferrugineuse à la bouche, rousse sur le pronotum, dont la base est étroitement et vaguement noirâtre, brun-noir sur les élytres, qui sont vaguement lavés de ferrugineux, les pattes et les antennes uniformément rousses. La ponctuation est extrêmement fine et indistincte sur la tête et le disque du pronotum, forte et assez serrée le long de la base du pronotum et sur les élytres dont la pubescence est couchée. Sur la tête, le bord posterior du clypeus est assez fortement élevé, par suite de la dépression transversale profonde qui le limite en arrière. Les hanches postérieures ont leur milieu couvert de points gros et peu serrés; l'apophyse prosternale est largement mais peu profondément canaliculée en son milieu, et

même chez certains exemplaires elle paraît presque plane; les lignes coxales sont, au contraire, très profondément imprimées. Les différences sexuelles sont très marquées et suffisamment indiquées dans la diagnose.

Trouvé dans les Tabacs provenant du Brésil."

***Bidessonotus peregrinus* sp. n. (fig. 9).**

Bidessus adumbratus Clark, Sharp, 1887, *Biol. Centr.-Amer.* 1 (ii), Suppl. : 754, nec Clark (*partim*).

Oblongo-ovalis, sat angustus, testaceus; capite testaceo, pertenuissime sat sparsim punctulato, laevigato; pronoto testaceo, ad basin inter plicas anguste vage infuscato, in medio tenuissime versus basin multo magis distincte et fortiore punctulato, sub-obsolete microreticulatio; elytris fusco-testaceis, vage nigricante maculatis, maris subnitidis, obsolete microreticulatis, feminae opacis, distincte microreticulatis, sub-iridescentibus; subtus testaceus, coxis posticis segmentisque basalibus abdominis lateraliter fortiter punctatis; tibiis intermediis maris subtus sinuatis, curvatis.

Head testaceous, very finely and quite sparingly punctulate, the interstices shining; transverse fronto-clypeal sulcus distinct though shallow at the sides, rather widely obsolete in the middle, particularly in the female; transverse cervical stria quite distinct though very fine. *Antennae* testaceous, longer and more slender in the male than in the female. *Pronotum* testaceous, at the base between the plicae narrowly and vaguely infuscate; on the disc very finely, at the base much more distinctly and strongly punctulate, sub-obsolete microreticulate; the sides weakly rounded, finely and distinctly margined; basal plicae oblique, almost straight, distinctly and quite strongly impressed, barely attaining one-half of the length of the pronotum from the base. *Elytra* ovate, posteriorly acuminate-attenuate at the apex in the male, more obtusely acuminate in the female; widest at middle, the sides weakly rounded; finely and moderately closely punctulate, the interstices about one and a half times the diameter of the punctures; moderately shining in the male, rather obsoletely microreticulate basally; quite dull, iridescent in the female, distinctly microreticulate, without trace of an epipleural tooth near the apex; epipleurs in the female barely discernibly explanate. *Venter* testaceous, finely microreticulate; prosternal process oblong, the apex rounded, distinctly and quite strongly longitudinally sulcate; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) quite strongly impressed; metacoxae and basal abdominal segments rather coarsely but not very closely punctate; apical ventrite very finely and moderately copiously punctulate, sub-nitid, finely microreticulate. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male distinctly incrassate; intermediate tibiae of the male curved, sinuate beneath, of the female straight beneath, triangular; intermediate femora of the male not at all produced into an obtuse tooth on the posterior edge of the ventral (tibial) furrow near the apex, at most gently roundly produced. *Aedeagus* with the median lobe adze-shaped, with both dorsal and ventral terminal angles sharp, sub-acute; lateral lobes with the distal piece scarcely bilaterally asymmetrical, obliquely truncate, proximal piece of the left lobe with a rounded-obtuse projection of the dorsal edge near the apex.

Size : 1.762-1.779 long., 0.882-0.898 mm. lat.

Holotype ♂, PANAMA : Pearl Islands, San Miguel (*Champion* coll.) (*Bidessus adumbratus* Clark, Sharp det.). Allotype ♀, same particulars as holotype.

This new species is quite distinct from the *championi*-group by the form of the apical piece of the median lobe of the aedeagus. It may be readily separated from *championi* by the distinctly interrupted transverse fronto-clypeal sulcus, the more shining male, the ventrally sinuate intermediate tibiae of the male, the quite undenticulate epipleurs of the female and the evidently smaller size. It is close to *obtusatus* Régimbart

and to *morosus* sp. n. in size and in character of the aedeagus, but it is perfectly distinct from each of these species by the shape of the intermediate femora of the male and by the apex of the median lobe of the aedeagus.

***Bidessonotus sobrinus* sp. n. (fig. 10).**

Bidessus adumbratus Clark, Sharp, 1887, *Biol. Centr.-Amer.* 1 (ii), Suppl. : 754, nec Clark (*partim*).

Elongato-ovalis, testaceus; capite testaceo, pertenuissime sat sparsim punctulato, sub-laevigato, obsolete microreticulato; pronoto testaceo, versus basin inter plicas lateraliter anguste infuscato, in medio tenuiter et obsolete, ad basin fortiore et multo distinctiore punctulato; elytris sordide testaceis, post basin, lateraliter et apicaliter vage pallidioribus, tenuiter parum crebre sat distincte punctulatis, tenuissime sed distincte microreticulatis, maris subnitidis, feminae opacis, vix iridescentibus, epipleuribus feminae postice vix explanatis, haud subapicaliter dentatis; subtus testaceus, processu prosternali anguste, distincte longitudinaliter canaliculato; metacoxis segmentisque basalibus abdominis lateraliter sat fortiter sat sparsim punctatis; tibiis intermediis maris subtus sat fortiter curvatis.

Head testaceous, extremely finely and quite sparingly punctulate, barely more strongly and densely so posteriorly, sub-nitid, obsoletely microreticulate; transverse fronto-clypeal sulcus moderately deep at the sides, widely obsolete in the middle; transverse cervical stria quite distinct. *Antennae* flavo-testaceous, slightly longer and more slender in the male than in the female. *Pronotum* testaceous, at the sides of the base between the plicae narrowly infusate; on the disc finely and obsoletely, near the base more strongly and much more distinctly punctulate; sub-nitid, obsoletely microreticulate, vaguely iridescent; the sides rounded, distinctly finely margined; basal plicae slightly oblique, almost straight, sharply impressed, not foveolate, attaining half the length of the pronotum from the base. *Elytra* dirty testaceous, behind the base, laterally and apically vaguely paler, a humeral, median and post-median ill-defined spot on the lateral declivity darker; finely and quite distinctly but not very closely punctulate, rather obsoletely so in the female, the interstices about one and a half to twice the diameter of the punctures; in the male sub-nitid, finely but distinctly microreticulate, in the female dull, scarcely iridescent, extremely finely microreticulate, the epipleurs in the female scarcely explanate behind, not longitudinally weakly canaliculate and not produced into a fine sub-apical tooth; ovate, the sides rounded weakly and widest at middle, apically rounded-attenuate, the sutural angle barely acuminate; basal plicae almost straight, finely, distinctly but not very strongly impressed, almost one and a half times the length of the pronotal plicae. *Venter* testaceous, microreticulate; the prosternal process narrow, apically rounded, quite strongly longitudinally sulcate; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) shallow but distinct; metacoxae and basal abdominal segments at the sides quite strongly but not very closely punctate; apical ventrite in the male finely, slightly obsoletely and moderately closely punctulate, in the female less finely and less closely punctulate. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male distinctly but not strongly incrassate; intermediate tibiae of the male moderately strongly curved; intermediate femora of the male quite strongly roundly, not at all angulate-produced on the hind margin of the ventral (tibial) furrow near the apex. *Aedeagus* with the median lobe axe-shaped, the "blade" narrow and rather curved, the "edge" widely rounded, at the apex of the shaft ventrally a small rounded, sub-transverse cristate process; the lateral lobes bilaterally asymmetrical, the distal piece of the right side larger than that of the left, terminally obliquely truncate, straight, the apical ventral angle quite rectangular; proximal piece of the left side widely obtusely angulate produced in the middle of the dorsal edge.

Size : 1.729-1.864 mm. long., 0.847-0.949 mm. lat.

Holotype ♂, PANAMA (without precise locality) (*Champion* coll.) (*Bidessus adumbratus* Clark, Sharp det.). Allotype ♀, same particulars as holotype. Paratypes: 1 ♀, same particulars as holotype; 1 ♀, PANAMA, 8.ii.1925 (*G. Bateson* coll.).

This small species is extremely closely related to *B. tibialis* Régimbart and to *B. morosus* sp. n., both described below, but it nevertheless appears to be perfectly distinct by the deeper transverse fronto-clypeal sulcus, the different form of the "blade" of the aedeagus, the appreciably narrower and more elongate form of the female compared to *tibialis*, the consistently different form of the aedeagus from *morosus*, the more shining male, the less obtusely rounded apex of the female, and the apparently shorter metacoxae than in *morosus*.

Bidessonotus morosus sp. n. (fig. 11).

Oblongo-ovalis, sat elongatus, testaceus; capite testaceo, pertenuissime sat sparsim punctulato, postice paulo crebriore et distinctiore, laevigato, feminae obsolete microreticulato; pronoto testaceo, ad basin inter plicas anguste nigricante; in medio tenuiter, versus basin fortiore et distinctiore punctulato; clytris griseo-testaceis, lateribus testaceis, ad humeros, ad medium et post medium indistincte fusco-maculatis; subtiliter parum crebre sat distincte punctulatis, maris sub-opacis, feminae opacis, sub-iridescentibus; epipleuribus feminae postice vix explanatis, haud sub-apicaliter denticulatis; subtus testaceus, processu prosternali anguste, ad basin fortiter longitudinaliter canaliculato; metacoxis segmentisque basalibus abdominis lateraliter grosse sat sparsim punctatis; tibiis intermediis maris subtus leviter curvatis.

Head testaceous, very finely and quite sparingly punctulate, a little more closely and distinctly so posteriorly, shining, in the female obsoletely microreticulate; transverse fronto-clypeal sulcus rather deep and distinct, shallow or narrowly obsolete in the middle; transverse cervical stria fine and rather indistinct. *Antennae* slightly longer and more slender in the male than in the female. *Pronotum* testaceous, the base between the plicae narrowly blackish; the sides weakly rounded, the margins fine but distinct; on the disc finely, towards the base more strongly and more distinctly punctulate; in the male obsoletely microreticulate between the plicae, sub-obsoletely between the plicae and the side margins, in the female very finely and somewhat obsoletely microreticulate, sub-iridescent; basal plicae oblique, weakly curved, sharply impressed, attaining rather more than half the length of the pronotum from the base. *Elytra* griseo-testaceous, behind the base widely, behind the middle and at the apex paler, an ill-defined humeral, median and post-median blackish spot on the lateral declivity; finely, quite distinctly and not very closely punctulate, the interstices from one and a half to twice the diameter of the punctures, finely but quite distinctly microreticulate in the male, quite dull, extremely finely microreticulate in the female, rather iridescent; oval, the sides rounded, widest at middle, the male rounded-attenuate apically, the sutural apices barely acuminate, the female posteriorly more obtusely rounded; epipleurs in the female posteriorly, weakly explanate, without trace of a sub-apical tooth; basal plicae almost straight, distinctly but not strongly impressed, about one and a quarter times the length of the pronotal plicae. *Venter* testaceous, finely microreticulate; prosternal process narrow, at the base deeply longitudinally canaliculate, the apex acutely rounded; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) finely but distinctly impressed; metacoxae and the basal abdominal segments at the sides strongly but quite sparingly punctate; apical ventrite in the male quite strongly and closely but shallowly punctulate, in the female more finely and less closely punctulate. *Legs* testaceous, the two basal segments of the anterior and intermediate tarsi of the male moderately strongly incrassate; intermediate tibiae of the male rather weakly curved beneath; intermediate femora of the male obtusely roundly produced on the posterior

edge of the ventral (tibial) furrow near the apex. *Aedeagus* with the median lobe axe-shaped, the "blade" narrow and rather curved, the "edge" obtusely rounded, at the apex of the shaft ventrally a small rounded sub-transverse cristate process; lateral lobes weakly bilaterally asymmetrical, the distal piece of the right side larger than that of the left, terminally widely rounded; the proximal piece of the left side widely rounded-obtusely produced in the middle of the dorsal edge.

Size : 1.830-1.932 mm. long., 0.779-0.983 mm. lat.

Holotype ♂, MEXICO : Sinaloa; Mazatlan, 1934 (H. E. Hinton, coll.). Allotype ♀, same particulars as holotype. Paratypes : 3 ♂, 1 ♀ same particulars as holotype.

Extremely closely related to *B. sobrinus* sp. n. but less elongate, broader in proportion to the length and duller, more distinctly and strongly microreticulate in the male, the intermediate tibiae in that sex less strongly curved beneath and the intermediate femora distinctly roundly-produced on the posterior edge of the ventral furrow near the apex.

Bidessonotus tibialis Régimbart (fig. 12).

Bidessonotus tibialis Régimbart, 1895, *Ann. Soc. ent. Fr.* 64 : 337.

Bidessus pulicarius Aubé, Sharp, 1882, *Sci. Trans. R. Dublin Soc.* 2 (ii) : 364 (partim).

Oblongo-ovalis, sat latus, testaceus; capite testaceo, antice sat sparsim tenuissime, postice paulo crebriore et distinctiore punctulato, laevigato; pronoto testaceo, ad basin inter plicas sat anguste vage infuscato, in medio tenuiter, versus basin fortiore et multo distinctiore punctulato; elytris griseotestaceis, post basin, post medium et apicaliter pallidioribus; lateraliter ad medium et post medium vage nigro-maculatis; tenuiter minus crebre et distincte punctulatis, subtiliter sub-obsolete microreticulatis, feminae vix iridescentibus; epipleuribus feminae postice haud explanatis, haud sub-apicaliter denticulatis; subtus testaceus, processu prosternali ovato, distincte longitudinaliter canaliculatis; metacois segmentisque basalibus abdominis lateraliter sat fortiter punctatis; tibiis intermediis maris subtus sat leviter curvatis.

Head testaceous, anteriorly quite sparingly and very finely, posteriorly a little more closely and more distinctly punctulate, shining; transverse fronto-clypeal sulcus shallow, very widely obsolete in the middle; transverse cervical stria very distinct. *Antennae* testaceous, evidently longer and more slender in the male than in the female. *Pronotum* testaceous, at the base between the plicae quite narrowly vaguely infuscate; on the disc finely, basally more strongly and much more distinctly punctulate, shining; basal plicae oblique, almost straight, sharply and quite strongly impressed, attaining rather more than half the length of the pronotum from the base; the sides basally almost straight, anteriorly rounded, finely distinctly margined. *Elytra* griseo-testaceous, behind the base widely, behind the middle and apically paler, at the middle and behind the middle on the lateral declivity with ill-defined blackish spots; finely fairly closely distinctly punctulate, the interstices about one and a half the diameter of the punctures; in the male quite distinctly finely microreticulate, in the female less distinctly and more finely, not very iridescent; the epipleurs in the female not at all explanate posteriorly, not at all denticulate before the apex; oval, the sides rounded, widest at middle; apically more obtusely rounded in the female than in the male; basal plicae almost straight, distinctly but not strongly impressed, about one and a half times the length of the pronotal plicae. *Venter* testaceous, finely microreticulate; prosternal process ovate, distinctly longitudinally canaliculate in the middle; metasternum impunctate, the anteriorly convergent sulci (anterior continuation of the coxal lines) shallowly impressed; metacoxae and basal abdominal segments at the sides fairly strongly punctate; apical ventrite in the male fairly strongly, moderately closely regularly punctate, of the female sparsely, fairly strongly punctulate, just before the apex smooth, shining. *Legs* testaceous, the two basal segments of the anterior and

intermediate tarsi of the male moderately strongly incrassate; intermediate tibiae of the male rather weakly curved beneath; intermediate femora of the male very obtusely produced on the hind margin of the ventral (tibial) furrow near the apex. *Aedeagus* with the median-lobe axe-shaped, the "blade" very narrow, the "edge" rather sharply rounded, at the apex of the shaft ventrally a small rounded, sub-transverse cristate process; the lateral lobes weakly bilaterally asymmetrical, the distal piece of the right side larger than that of the left, terminally transversely truncate, the ventral apical angle rectangular; the distal piece of the left side obliquely truncate, the terminal ventral angle obtuse; proximal piece of the left side widely obtusely produced in the middle of the dorsal edge.

Size: 1.779-1.898 mm. long., 0.915-0.983 mm. lat.

Redescribed from 1 ♂, 1 ♀, BRAZIL: Santa Rita, August, 1850, "324" (*Sahlberg* coll.) (*Hydroporus* ? *pulicarius* var. Sharp det.). 1 ♂, BRAZIL: Matto Grosso, Porto Velho, viii-ix.1937 (*H. E. Hinton* coll.).

Extremely close to *B. sobrinus* sp. n. in many respects and closer thereto than the third species *mosorus* of this group. The very shallow, widely interrupted fronto-clypeal sulcus, the less curved intermediate tibiae of the male and the distinct aedeagus seem to characterise the present species satisfactorily. The wide geographical separation from the two closely related species may prove to be more apparent than real on further careful collecting in northern South America.

LIST OF THE SPECIES OF *BIDESSONOTUS* RÉGIMBART.

- | | | | | | |
|-------------------------------------|----------------------------------|-----|-----|-----|--------------------------|
| 1. <i>régimbarti</i> nom. nov. | ... | ... | ... | ... | "Mexique." |
| <i>adumbratus</i> (Clark) | Régimbart, nec Clark, nec Sharp. | | | | |
| 2. <i>mobilis</i> sp. n. | ... | ... | ... | ... | Mexico: Tabasco. |
| <i>adumbratus</i> (Clark) | Sharp <i>partim</i> , nec Clark. | | | | |
| 3. <i>fallax</i> sp. n. | ... | ... | ... | ... | Cuba: Sta. Clara Prov. |
| 4. <i>vicinus</i> sp. n. | ... | ... | ... | ... | British Honduras. |
| 5. <i>longovalis</i> (Blatchley) | ... | ... | ... | ... | U.S.A., Florida. |
| 6. <i>inconspicuus</i> (LeConte) | ... | ... | ... | ... | U.S.A., Louisiana. |
| 7. <i>pulicarius</i> (Aubé) | Sharp <i>partim</i> | ... | ... | ... | U.S.A., Florida. |
| <i>subsericeus</i> (Blatchley) | syn. nov. | | | | |
| 8. <i>caraibus</i> (Chevrolat) | ... | ... | ... | ... | "Cuba." |
| 9. <i>championi</i> sp. n. | ... | ... | ... | ... | Guatemala: Paso Antonio. |
| <i>adumbratus</i> (Clark) | Sharp <i>partim</i> nec Clark. | | | | |
| 10. <i>mexicanus</i> Régimbart | ... | ... | ... | ... | Mexico: Teri. |
| 11. <i>obtusatus</i> Régimbart | ... | ... | ... | ... | Brazil: Santa Rita. |
| <i>pulicarius</i> (Aubé) | Sharp <i>partim</i> | ... | ... | ... | Paraguay; Bolivia. |
| 12. <i>truncatus</i> sp. n. | ... | ... | ... | ... | Brazil: Porto Alegre. |
| 13. <i>nepotinus</i> sp. n. | ... | ... | ... | ... | Trinidad: St. Augustine. |
| 14. <i>browneanus</i> sp. n. | ... | ... | ... | ... | Jamaica: Gayle. |
| 15. <i>melanocephalus</i> Régimbart | ... | ... | ... | ... | "Bresil." |
| 16. <i>peregrinus</i> sp. n. | ... | ... | ... | ... | Panama: Is. Perlas. |
| <i>adumbratus</i> (Clark) | Sharp <i>partim</i> , nec Clark. | | | | |
| 17. <i>sobrinus</i> sp. n. | ... | ... | ... | ... | Panama. |
| <i>adumbratus</i> (Clark) | Sharp <i>partim</i> , nec Clark. | | | | |
| 18. <i>mosorus</i> sp. n. | ... | ... | ... | ... | Mexico: Sinaloa. |
| 19. <i>tibialis</i> Régimbart | ... | ... | ... | ... | Brazil: Santa Rita. |
| <i>pulicarius</i> (Aubé) | Sharp <i>partim</i> . | | | | |

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ON THE REDUCTION OF FUNCTIONAL SPIRACLES IN THE AQUATIC LARVAE OF THE HOLOMETABOLA, WITH NOTES ON THE MOULTING PROCESS OF SPIRACLES

BY H. E. HINTON, PH.D.

Department of Entomology, British Museum (Natural History).

Manuscript received 27th January, 1947.

(Read 4th June, 1947.)

WITH 5 TEXT-FIGURES.

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INTRODUCTION.

SOME years ago I published (Hinton, 1939*a*, 1939*b*) the results of my studies on the interrelations of the DRYOPIDAE, ELMIDAE, and allied families of Coleoptera. The discovery at that time of the larva of *Eubria palustris* L. by Bertrand (1939) served to emphasise the need for more information on the relation of the Dryopoidea to the Dascilloidea and other superfamilies. In order to make a further contribution to this subject, work was begun on the spiracular structures and respiratory adaptations of the larvae and pupae, and a paper on this subject is being published elsewhere. A study of the spiracles of the larvae showed that a definite pattern existed in the ontogenetic sequences of functional and non-functional spiracles. It was then necessary to discover if the ontogenetic sequences of functional spiracles observed in the Dryopoidea were peculiar to these insects, and if not, to what extent they applied to all aquatic larvae. This paper is one result of an attempt to answer this question.

II. GENERAL CONSIDERATIONS.

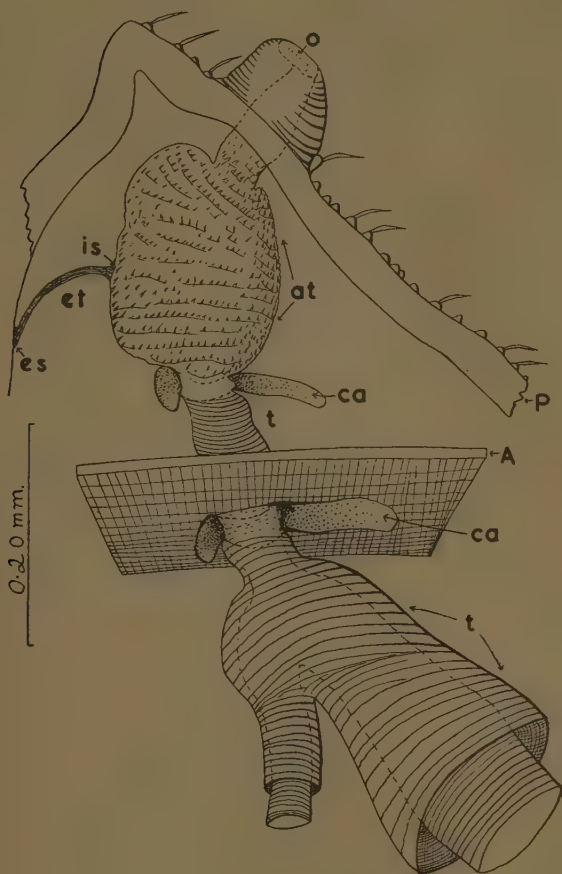
The ontogeny of all insects consists of a series of alternating exuvial and cuticular phases—that is, phases when the epidermal layer is not

intimately bound to the cuticle (exuvial) alternating with phases when it is so connected (cuticular). Each instar begins as an exuvial phase of relatively short duration and is followed by a cuticular phase of relatively long duration. The beginning of the loosening of the cuticle and the freeing of the epidermis initiates a new instar. In the exuvial or first phase of the new instar, the epidermal layer may change considerably in form and there may be extensive neo-formations, most of which take place before the secretion of a new cuticle. These changes determine the form of the new instar. Sometime after the formation of the new cuticle, which bears the various cuticular processes characteristic of the new instar, the old cuticle is shed.

The tracheo-spiracular system of each segment which bears a spiracle is formed at a comparatively late stage in the embryo as an invagination of the ectoderm. The appearance of the tracheal invaginations usually coincides more or less with the first segmentation of the mouth-parts and legs. In many apterygote and probably all pterygote insects the principal, usually one or two, longitudinal trunks of each tracheo-spiracular metamere fuse together to form a single tracheal system on each side. In most, the right and left tracheal systems are united in varying degrees of complexity by the fusion of the transverse commissures of the opposite sides of one or more segments.

The exocuticle of the tracheal walls has a very characteristic and more or less continuous spiral ridge-like thickening. The form of the spiral thickenings (taenidia) varies little from one insect to another, but a few striking exceptions have been described. The spiral thickening is a device which enables the tracheae to withstand lateral pressure while at the same time permitting considerable stretching. The spirally thickened tracheae do not extend from the surface, but between the surface and the tracheae proper there is a tube of varying length which is known as the spiracle. In its primitive form the spiracle is a simple tube with an external opening at the surface and an internal opening into the tracheae. In many insects the spiracle is highly specialised and may have a number of different openings to the surface. The shape of the tube or spiracular chamber (atrium) and the form of the cuticular processes projecting from its walls into the lumen are very variable; and they may differ greatly not only from one insect to another but frequently between the various stages of the same species. The walls of the spiracular chamber rarely have a spiral type of thickening (fig. 2), but even in such instances the spiral thickening is usually easily distinguished from that of the tracheae proper.

In most pterygote insects a part of the spiracular chamber is modified to form a closing apparatus which is always, so far as I know, located immediately before the tracheal orifice. The distance of the closing apparatus from the surface of the body thus depends on the length of the spiracular chamber. A good example of this is shown in fig. 1, where the closing apparatus is far from the surface in the pupa and just below the surface in the adult. The absence of a closing apparatus in the recent Pterygota is probably always to be regarded as a secondary or specialised feature. Among the Holometabola it is absent, for instance, in the larvae



1

FIG. 1.—*Eubria evansi* Hinton (PSEPHENIDAE).

Third abdominal segment of pharate adult to show relationship of pupal to adult spiracles.

The pupa has the specialised elateroid type of spiracle and the adult the primitive type of spiracle. The non-functional spiracle of the larva is on the ventral part of the pleural extension, and the ecdysial opening of the pupa was formed at a corresponding position (*es*) in the similarly shaped pupa. The functional opening of the pupal spiracle (*o*) is on the dorsal surface almost exactly above the temporary ventral opening of the ecdysial tube through which the larval tracheae were withdrawn.

A, Adult cuticle; **at**, spiracular chamber or atrium; **ca**, closing apparatus; **es**, external scar of ecdysial opening of pupa, sometimes known as the stigmatic scar; **et**, pupal ecdysial tube; **is**, internal scar of ecdysial opening; **P**, pupal cuticle; **o**, functional opening of pupal spiracle; **t**, tracheae.

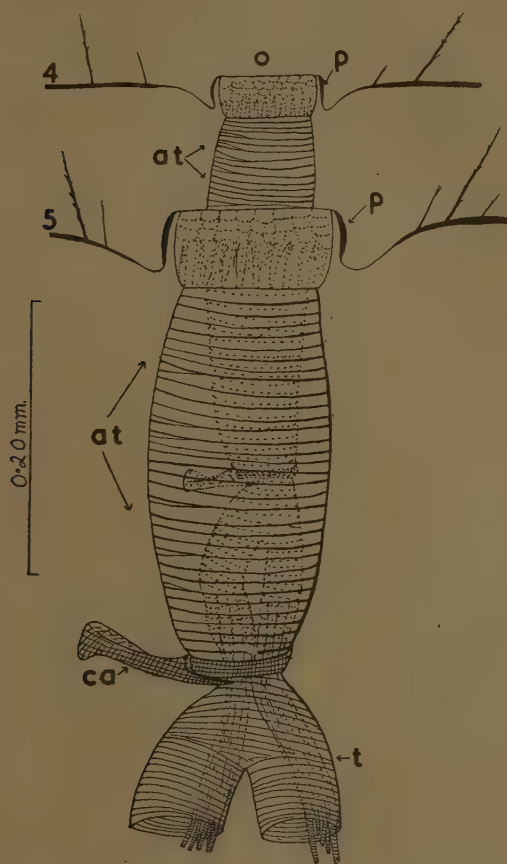
of a number of Coleoptera and Diptera, but it is apparently always present in the imagines of the same groups.

In the Holometabola departures from the primitive type of spiracle are greater in degree and more frequent in the larvae than in the adults, and in a broad general way it may be said that the spiracles of the larvae tend to become more specialised than those of the imagines, which is but a reflexion of the fact that the larvae have successfully invaded a much wider range of habitats. The spiracles of the pupa or first imaginal instar are, as a general rule, slightly nearer the primitive type than those of the imago or second imaginal instar, but there are many exceptions to this rule. For instance, the first thoracic spiracles of the aquatic pupae of the Diptera are always very different from those of the larvae or adults of the same species, and this is also true of the abdominal spiracles of some aquatic coleopterous pupae—e.g., *Psephenoides*. The first thoracic spiracles of many terrestrial dipterous pupae—e.g., the TIPULIDAE—are also very different from those of the larvae or adults of the same species. In some pupae the structure of the spiracles may be somewhat like those of the larvae but very different from those of the adults—e.g., a few Coleoptera (Eubrini, many LYCIDAE).

The spiracles and tracheae are moulted in the same way and at the same time as the cuticle elsewhere on the body. At the conclusion of the cuticular phase of any instar, a moulting hormone is secreted which initiates the secretion of an ecdysial or moulting fluid by the epidermis and special epidermal glands. This fluid in due course dissolves the endocuticle and completely frees the epidermis from the exocuticle of the general body surface as well as from the internal cuticular parts such as the lining of parts of the gut, the tentorium and other apodemes, and the tracheae and spiracles. The space between the exocuticle and the epidermis effects the continuity of the moulting fluid in all parts of the body, since the internal cuticular parts are secreted by simple invaginations and internally directed proliferations of the cuticle-secreting epidermis of the outer body wall. Before the secretion of a new cuticle, there may be extensive proliferations of the epidermis to produce the structures characteristic of the new instar. Before the secretion of a new cuticle, the epidermis contracts away from the enveloping cuticle. This contraction in the exuvial phase is usually slight between larval instars, but may be very considerable in the larva to pupa or pupa to adult moults. This epidermal contraction is of great significance for a clear understanding of the moulting of some specialised spiracles and the migration of others from one part of a segment to another.

The cuticular phase of an instar begins by a secretion of a new cuticle. In the case of the tracheae and spiracles, the newly secreted cuticle surrounds these structures belonging to the previous instar; and for this reason the position of the tracheae in any particular instar is largely predetermined by their position in the previous instar, although new extensions of the tracheae produced by new proliferations of the epidermis may arise in each instar. As it is impossible for the new spiracle to be secreted exactly around the old spiracle, the new spiracle

is always slightly displaced internally in relation to the old. The internal displacement of the new spiracle is slightly or considerably increased according to the degree of contraction of the epidermis from the exocuticle of the body wall. In many cases, for instance, the peritreme of the new spiracle may be secreted at the level of the internal opening of the old spiracular chamber.



2

FIG. 2.—*Dermestes maculatus* Degeer (DERMESTIDAE).

Moult between fourth and fifth larval instars to show the moulting process of the primitive type of spiracle. The walls of most of the spiracular chamber (*at*) are unusual in being spirally thickened like the tracheae, but more coarsely so.

at, Spiracular chamber or atrium; *ca*, closing apparatus; *o*, functional opening of fourth instar; *P*, peritreme; *t*, tracheae.

When the old cuticle is shed, the old spiracles and usually all but the finer branches of the tracheae are withdrawn through the newly formed spiracles and tracheae which enclose them. The old spiracles and tracheae remain attached to the old cuticle. The tracheae and spiracles of each segment are withdrawn through the new spiracles of the corresponding segments. In order to be withdrawn, the old tracheal system must break in a number of places, but it is not known if these breaks are at the original points of fusion of the tracheal metameres.

A. *Moulting process of primitive spiracles.*

The primitive type of spiracle is moulted as shown in fig. 2. A simple withdrawal of the old tracheae through the functional opening of the newly formed spiracle also occurs in many insects with comparatively specialised spiracles so long as the external opening of the spiracle or the cuticular processes of the spiracular chamber permit withdrawal of the old tracheae. In the Holometabola this primitive method of moulting occurs between the larval moults of the majority of species and apparently also in all pupa to adult moults. In the larva to pupa moults it is the rule except in some Coleoptera and Diptera that have pupae with spiracles so specialised that the formation of a special ecdysial tube for the withdrawal of the larval tracheae from the pupa is necessary for mechanical reasons. In short, it may be said that the primitive method of moulting obtains wherever the new spiracular opening and chamber are not sufficiently blocked with cuticular processes to prevent withdrawal of the tracheae of the previous instar.

B. *Moulting process of highly specialised spiracles.*

The moulting process of the two principal kinds of highly specialised larval spiracles found in the Diptera has been clearly described by de Meijere (1894) and Keilin (1944). From an examination of a large number of larvæ of other holometabolous orders, it appears that there are no more than two basic types of highly specialised spiracles. Very few (mainly beetles) have actually been observed by me in the process of moulting, but the structure of the spiracles rarely leaves any doubt as to the exact method of moulting. For convenience in referring to the two kinds, I have called the first the "panorpid" and the second the "elateroid." Both kinds appear to have been evolved independently from the primitive type.

(1) *Moulting process of panorpid spiracles.*

In the panorpid spiracle, common in the Mecoptera and Diptera Orthorrhapha, the peripheral part of the spiracular plate usually consists of a cuticular membrane in which there are numerous fine clefts or tubes through which air is drawn. The membrane is usually reinforced by stout cuticular rods. In this kind of spiracle it is obvious that the membrane and rods absolutely prevent the withdrawal of the tracheae of the old instar through the openings used for the intake of air. The development of a specialised obstructed spiracular opening is only possible if the new cuticular modifications in structure develop *pari passu* with new methods for the withdrawal of the old spiracle and tracheae when the cuticle is



3

FIG. 3.—*Ctenophora ornata* Meigen (TIPULIDAE).

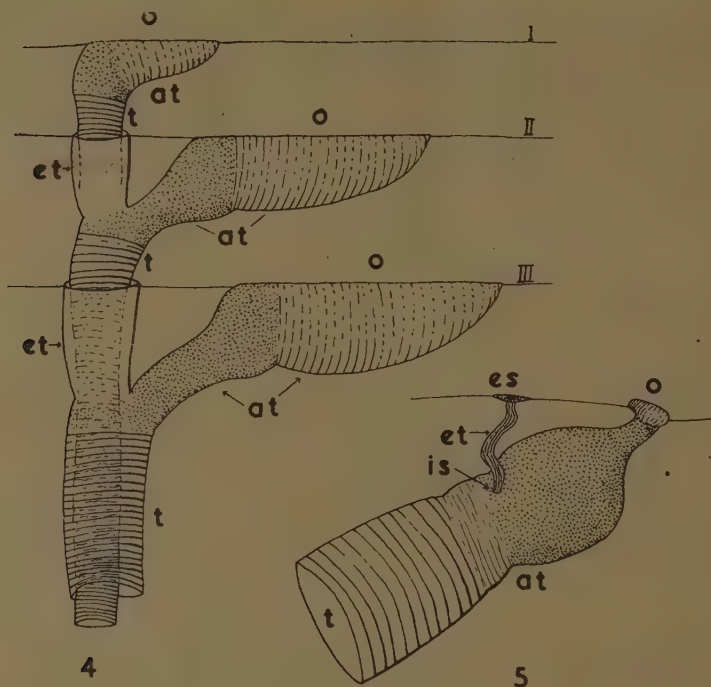
Longitudinal section through eighth abdominal spiracle to show the specialised panorpoid type of spiracle.

at, Spiracular chamber or atrium; o, functional openings; s, heavily sclerotised cuticle closing the temporary ecdysial opening in centre of spiracular plate. (After Keilin.)

shed. The specialised opening of the new instar spiracle is formed around the outside of the spiracular chamber of the previous instar. The spiracular chamber and tracheae of the previous instar are withdrawn through this central ecdysial opening. This opening is later closed by "the contraction and hardening of the chitin surrounding the ecdysial opening (Keilin, 1944, p. 5)," and its former position is marked by a solid sclerotised area in the centre of the spiracle. It is clear that, whatever its history, the moulting process of this kind of spiracle now differs but little from the primitive method.

(2) Moulting process of elateroid spiracles.

The second principal kind of specialised spiracle, the elateroid, is common in the Coleoptera and Diptera. In the Coleoptera, for instance, it has been independently evolved at least six times. The functional opening of the second and successive larval instars is formed to one side of a simultaneously formed simple cuticular tube (the ecdysial tube) which encloses the lower part of the spiracular chamber, or the tracheae immediately below, of the previous instar (fig. 4). When the old cuticle is shed, the old tracheae are withdrawn through the ecdysial tube which opens internally into the spiracular chamber of the new instar. After



FIGS. 4-5.

- (4) *Dryops* sp. (DRYOPIDAE). Diagrammatic figure of moults between first and second and second and third larval instars to show the moulting process of the elateroid type of spiracle.
- (5) *Eubrianax* sp. (PSEPHENIDAE). Mature larva showing the closed and collapsed ecdysial tube through which the tracheae of the penultimate instar were withdrawn.
- at, Spiracular chamber or atrium; es, external scar of ecdysial opening; et, ecdysial tube; is, internal scar of ecdysial opening; o, functional opening; t, tracheae.

the old cuticle is shed, the ecdysial tube collapses, and both its internal and external openings are more or less completely closed. The closed external opening appears in most forms as an easily recognisable scar (the stigmatic scar) behind or to one side of the functional opening, and it may be located very close to the functional opening or a considerable distance away (fig. 1). For instance, in the ELATERIDAE it is very close to the functional opening in *Chalcolepidius* and very far from it in some *Agriotes*. Both Steinke (1919) and Böving and Craighead (1931) have consistently mistaken the stigmatic scar for the true functional opening. The moulting process for this type of spiracle is shown in fig. 4. The spiracular plates of some SCARABAEIDAE, particularly Dynastids, bear a close superficial resemblance to the panorpoid type, but the method of moulting in the SCARABAEIDAE appears to be essentially similar to that of the ELATERIDAE.

C. Significance of non-functional spiracles.

The primitive and specialised spiracles described in the preceding paragraphs are all functional. Their external openings may be widely open, partly closed in a variety of ways, or they may be completely closed by a cuticular membrane permeable to gases. During all or some part of the life of the instar that bears them, the functional spiracles will actually be used under normal conditions to take in oxygen. In many aquatic and endoparasitic larvae, as well as in a few others, one or more pairs of spiracles are non-functional in the sense that they are not used by the insect for taking in air. The significance of the persistence of these non-functional spiracles was first clearly shown by Palmén (1877). Each non-functional spiracle consists of a surface scar (sometimes very difficult to see) precisely similar to the stigmatic scar of the elateroid spiracle. To the internal surface of the scar is attached a more or less solid, nearly transparent cuticular filament which is internally joined to a trachea. The moulting process of these spiracles is essentially as in the primitive type of spiracle.

At the beginning of the cuticular phase of an instar, the epidermal cells surrounding the non-functional filament secrete a cuticular tube which contains within its lumen the non-functional filament of the previous instar. The lumen of this cuticular or ecdysial tube is continuous with that of the newly secreted tracheae which envelop the tracheae of the previous instar. When the cuticle of the previous instar is shed, the non-functional filament, which is firmly attached to the non-functional spiracular scar, pulls out the old tracheae through the new tracheae and ecdysial tube. After withdrawal of the tracheae of the previous instar, the newly formed ecdysial tube collapses and its lumen is lost. Shortly after ecdysis the external opening of the ecdysial tube, which is morphologically equivalent to the external opening of the primitive type of spiracle, is more or less completely closed by what is apparently a centripetal contraction of the peripheral cuticle. These "non-functional" spiracles are non-functional only in the sense that they are not used for taking in air. Without them the insect would be quite unable to expel the old tracheae at ecdysis; and probably for this reason—the mechanical expulsion of the old tracheae—they have been preserved in larvae which are apneustic in all instars.

It should be noted that the non-functional spiracles of each instar play an important part in ecdysis at two different times: (1) when they are first formed their chambers (ecdysial tubes) provide a lumen and an external opening through which the old tracheae may be withdrawn; and (2) after the appearance of a new instar their chambers, now collapsed, are the means by which the tracheae are anchored to the cuticle that is to be shed.

From a study of the development of different respiratory systems in the *Diptera*, Keilin (1944, p. 31) has proposed the following generalisations:—

1. "The tracheo-spiracular apparatus of the larva is already complete at the time of its hatching from the egg—i.e., all the tracheo-

spiracular metameres are present, arising from either functional or non-functional spiracles."

2. "In all stages, the total number of spiracles [functional plus non-functional] and of the tracheo-spiracular metameres is ten pairs, and this applies to all respiratory systems."

3. "The spiracles which become functional after a moult, are always formed from pre-existing spiracles and their branches, which may or may not have been functional; no spiracle ever appears independently of a corresponding spiracle of the previous stage."

All larvae of the Megaloptera, Neuroptera, Mecoptera, Lepidoptera, Coleoptera, and Hymenoptera which I have been able to study conform to Keilin's generalisations. So far as the first is concerned, various writers have stated that no tracheal system exists in some newly hatched endoparasitic Diptera and Hymenoptera. If this should indeed prove to be the case, it can hardly be an exception to the first generalisation, since these forms are correctly regarded (Berlese, 1925; Imms, 1936; Henson, 1946) as precociously hatched embryos rather than as definitive larval forms. In *Chironomus*, however, it appears that the tracheal system does not develop until the late larval stages (Johannsen and Butt, 1941). Although the tracheo-spiracular metameres are complete in the sense that all are represented in the young larva, considerable alterations and additions may occur in subsequent larval instars and in the pupa and adult. There are a few exceptions to the second generalisation: in some JAPYGIDAE there are eleven pairs of spiracles (four in the thorax) and in other Entognatha less than ten pairs. Among the Pterygota, no well-authenticated exceptions are known. Although many Hemiptera have lost one or more pairs of functional spiracles, I am unable to say whether or not a sufficient number of reduced non-functional spiracles are present (but overlooked by writers) to bring the total number up to ten.

Functional and non-functional spiracles coexist in all holometabolous larvae with the exception of a few holopneustic forms (BIBIONIDAE, Siphonaptera). In some larvae—*e.g.*, some HYDROPHILIDAE—the meta-thoracic spiracles are non-functional, those of the eighth abdominal segment belong to the primitive type, and the remainder belong to the elateroid type.

III. REDUCTION OF SPIRACLES.

A. Generalisations concerning the ontogenetic sequences of functional spiracles in aquatic holometabolous larvae.

There can be no doubt that holometabolous larvae are primitively terrestrial and that the primitive number of functional spiracles is at least nine. It therefore follows that the aquatic habit and any structural modifications, such as a reduction in the number of functional spiracles, resulting from life in the water may be regarded as secondary. One of the most characteristic and universal structural alterations undergone by the aquatic larvae of the Holometabola is a reduction in the number of functional spiracles. In a broad general way, the degree to which the functional spiracles are reduced is an indication of the degree to which the

larva is adapted to life in the water; and the success with which this rule may be applied varies directly with the degree of the genetic relationship of the groups being compared, providing only that these have essentially the same habits in the water.

In Table 1 is shown the distribution of the functional spiracles in all the principal groups of aquatic holometabolous larvae. Most of the information on the Diptera has been taken from Keilin (1944). For much of the information regarding the Lepidoptera I have had to rely on published accounts, but I have been able to examine two South American species of gill-bearing *Nymphula*. All others have been examined by myself except AGRIOTYPIDAE (Clausen, 1940), HYDROSCAPHIDAE (Böving, 1914), and *Lissorhopterus* (Isely and Schwardt, 1930). Although a few inaccuracies will no doubt be found in Table 1, and although there are many assumptions (all marked with an asterisk) in the column listing the distribution of the spiracles in the first instar, I do not believe further information is likely to alter materially the main conclusions given below regarding the reduction of the functional spiracles.

The distribution of the functional spiracles in the successive instars of the several groups of aquatic holometabolous larvae shown in Table 1 makes it possible to formulate a few important generalisations:—

(1) Whenever there is a difference in the number of functional spiracles in two instars, the number of functional spiracles of the earlier instar is less than that of the later instar. Since in the primitive tracheal system all the spiracles are functional, departures from this condition may correctly be regarded as secondary specialisations. It therefore follows that every known change in the number of functional spiracles in the successive larval instars of one species is a non-recapitulative change.

(2) Whenever the spiracular system is apneustic in one instar, it is apneustic in all previous instars. There is no known exception to this rule, which is a necessary corollary to the first generalisation. While the possibility of an exception to this rule cannot be absolutely excluded, it is a good working hypothesis that when the final larval instar of an aquatic species is apneustic all previous instars will likewise be apneustic.

(3) An apneustic first instar in no way predetermines the number of functional spiracles that will be present in the final instar. A larva which is apneustic in its first instar may have 0–9 pairs of functional spiracles in its final instar.

(4) An apneustic first instar is nearly always followed by apneustic intermediate instars, but the final instar may have one or more pairs of functional spiracles. In the same way first instar larvae having one or more pairs of functional spiracles are succeeded by intermediate instars having the same number of functional spiracles. The only exceptions to this rule that I know of are some aquatic cyclorrhaphous Diptera.

(5) Since aquatic holometabolous larvae which are holopneustic do not appear to exist, it follows from (1) that when the first instar is peripneustic, all succeeding instars will likewise be peripneustic.

Generalisations (1), (2), and (3) contradict the law of recapitulation.

TABLE I

The distribution of the functional spiracles in the aquatic larvae of the Holometabola.

	Instars		
	First	Intermediate	Final
Megaloptera (<i>Archichauliodes</i>) ¹	?	S _{II+1-8}	S _{II+1-8}
" (<i>Corydalis</i>)	N*	N	S _{II+1-8}
" (<i>Sialis</i>)	N	N	S _{II+1-7}
Neuroptera, SISYRIDAE	?	?	S _{II+1-8}
Diptera, TIPULIDAE	S ₈	S ₈	S ₈
" " (<i>Antocha</i>)	N	N	N
" PTYCHOPTERIDAE	S ₈	S ₈	S ₈
" ANISOPIDAE	S ₈	S ₈	S ₈
" BLEPHAROCERIDAE	N	N	N
" SIMULIDAE	N	N	N
" CHIRONOMIDAE	N	N	N
" CERATOPOGONIDAE	N	N	N
" CULICIDAE	S ₈	S ₈	S ₈
" " (<i>Chaoborus</i>)	N	N	N
" TABANIDAE	S ₈	S ₈ ?	S _{I+8}
" STRATIOMYIDAE	S ₈	S ₈ ?	S _{I+8}
" SYRPHIDAE (most)	S ₈	S _{I+8}	S _{I+8}
" " (root-piercers)	S ₈	S ₈	S ₈
" EPHYDRIDAE (many)	S ₈	S ₈	S ₈
Trichoptera	N	N	N
Lepidoptera, ARCTIIDAE	S _{I+1-8} *	S _{I+1-8}	S _{I+1-8}
" PYRALIDAE (<i>Nymphula</i> <i>obliteralis</i> Walker) ²	?	?	S _{I+1-8}
" PYRALIDAE (<i>Nymphula</i> <i>maculalis</i> Clemens)	N*	N*	S ₁₋₃
" PYRALIDAE (<i>Nymphula</i> 2 spp. S. America)	N*	N	S _{I+1-8}
" PYRALIDAE (<i>Nymphula</i> <i>stratiotata</i> L.)	N	N	S ₁₋₃
" " (<i>Cataclysta</i>)	?	?	S _{I+1-8}
" " (<i>Acentropus</i>)	N	N	N
" AGROTIDAE (<i>Bellura</i>)	S _{I+1-8} *	S _{I+1-8} *	S _{I+1-8}

All assumptions are indicated by an asterisk ; and they are based on the five generalizations listed on p. 459.

¹ In the mature larva of *Archichauliodes diversus* Walker the peritreme of the meta-thoracic spiracle is well developed. From an examination of preserved specimens it seems certain that S_{II} is non-functional. The BIBIONIDAE and Siphonaptera are the only known holopneustic larvae in the Holometabola.

² Welch (1922) has attempted to show that nine pairs of spiracles are functional in a number of North American aquatic larvae of the PYRALIDAE. He has not envisaged the possibility that they might be functional in one instar and not in another. From the evidence presented in his paper, I have come to very different conclusions, which are supported by the two South American species of *Nymphula* I have been able to examine. I have little doubt that all gill-bearing species of *Nymphula* and *Cataclysta* will be found to have apneustic early instars.

	Instars		
	First	Intermediate	Final
Hymenoptera, AGROTYPIDAE ³	N	N	S _{I+1-8}
Coleoptera, GYRINIDAE ⁴	N	N	S ₁₋₃
" DYTISCIDAE	S ₈	S ₈	S _{II+1-8}
" AMPHIZOIDAE	S ₈ *	S ₈	S _{II+1-8}
" HYGROBIIDAE ⁵	N	N	S _{II+1-7}
" NOTERIDAE ⁶	S ₈ *	S ₈	S ₁₋₈
" HALIPLIDAE	N	N	S _{II+1-7}
" HYDRØPHILOIDEA (most)	S _{II+1-8}	S _{II+1-8}	S _{II+1-8}
" " (Berosini)	N	N	S _{II+1-8}
" " (SPERCHEIDAE)	?	?	S _{II+1+8}
" HYDROSCAPHIDAE ⁷	?	?	S _{I+1+8}
" DRYOPIDAE	S _{II+1-8}	S _{II+1-8}	S _{II+1-8}
" ELMIDAE	N	N	S _{II+1-8}
" LIMNICHIDAE (<i>Lutrochus</i>)	N*	N	S _{II+1-8}
" PTILODACTYLIDAE	N*	N	S _{II+1-8}
" PSEPHENIDAE (<i>Psephenus</i> and <i>Eubrianax</i>)	S _{II+8}	S _{II+8}	S _{II+8}
" " (some Eubrini)	S ₈ *	S ₈	S ₈
" " (other Eubrini)	N*	N	S ₈
" " (<i>Psephenoides</i>)	N*	N	N
" EULACHIDAE	?	?	S _{II+1-8}
" HELODIDAE	S ₈ *	S ₈	S ₈
" LAMPYRIDAE (gill-bearing)	?	?	S _{II+1-7}
" CHRYSOMELIDAE (Donacini)	S ₈	S ₈	S _{II+1-8}
" CURCULIONIDAE (<i>Lissorhopterus</i>)	?	?	S _{II+1-8}

All assumptions are indicated by an asterisk ; and they are based on the five generalizations listed on p. 459.

³ This is based on the summary given by Clausen (1940). Only two species of AGROTYPIDAE are known. *Agrotypus armatus* Walker is said to be apneustic in its final instar, but Clausen believes that this is unlikely to be true.

⁴ Schiödt (1861) and others claim that the larvae of the GYRINIDAE are apneustic in all instars. Steinke (1929) says that some of the spiracles are more atrophied than others, but he does not distinguish between functional and non-functional spiracles. I have examined two species of *Gyrinus*, one *Orechtochilus*, and one *Dineutus*.

⁵ The third instar of *Hygrobia hermanni* F. is not apneustic as stated by Balfour-Browne (1922), but has well-developed functional spiracles on the mesothorax and first seven abdominal segments.

⁶ According to Bertrand (1927, pp. 183, 196), the mesothoracic spiracles are functional. I have been able to examine third instar larvae of *Hydrocanthus* and *Noterus*, and in both genera there are no functional thoracic spiracles.

⁷ Böving (1914) says that the spiracles are absent in *Hydroscapha*, but his figure plainly shows the prothoracic and first and eighth abdominal spiracles, which are exceptionally well developed. It is clear from Böving's figures that the spiracles of *Hydroscapha* are most unusual in form. The only other beetle larva that I know of with similar spiracles is an Elmid (Larini, gen. ?) I collected in French Guiana. It is possible that a more careful study of *Hydroscapha* will show that the second to seventh abdominal segments also possess functional spiracles.

Exceptions to the law of recapitulation are numerous and often recorded, but all exceptions appear to be due to the selection of adaptive features which obscure or altogether suppress the expected recapitulative sequences. The adaptive non-recapitulative sequences recorded in Table 1 owe their origin to the unequal function of the spiracles in different instars, this unequal function being positively correlated with structural differences.

The fact that in a large proportion of aquatic larvae ontogenetic differences exist in the number of functional spiracles is proof positive that in these larvae the mode of obtaining oxygen differs in different instars. As spiracles cannot, because of their minute surface area, assume a significant role in respiration so long as the larvae are beneath the surface of the water, it seems clear that the instars which have the greatest number of spiracles must be better adapted to an aerial life than those which have fewer functional spiracles. A difference in the number of functional spiracles between two larval instars of the same species implies a difference in the adaptation of the two instars to life in the water. The fact that an increase in the number of functional spiracles nearly always occurs in the final instar, is a plain indication that the final instar is not as strictly aquatic as the early instars, and the retention of a greater number of functional spiracles in this instar is an adaptation to passing at least some of its life out of water. A few examples of the life-histories of aquatic insects will suffice to show that this is so.

(1) In the CORYDALIDAE, the early instars (the first has not been seen) of *Corydalis* are apneustic and remain beneath the surface of the water where they breathe by means of abdominal gills. The final instar also has gills but is peripneustic. The full-fed final instar larva of *Corydalis* leaves the water in order to construct a pupal chamber in the earth or sand, usually under a stone; and it is for use at this time that the functional spiracles have been retained. Another Corydalid which I have examined, *Archichauliodes diversus* Walker, is peripneustic in its early instars as well as in its final instar. In a study of the biology of *A. diversus*, Hamilton (1940) has shown that, unlike *Corydalis*, the larva leaves the water at each moult, and, after the completion of the moult, returns again to the water. It leaves the water for the last time in order to pupate on land. The fact that each instar passes some of its life out of the water would appear to account for the retention of a peripneustic system in all instars. *Archichauliodes* thus appears to be more primitive than *Corydalis*, an assumption supported also by the fact that in addition to the lateral abdominal gills *Corydalis* also has some multi-branched more ventral gills on the abdomen. The habit of *Archichauliodes* of coming out of the water at the end of each larval instar is unique.

(2) In the SIALIDAE, the early instars of *Sialis lutaria* (L.) are apneustic, but the final instar larva has the mesothoracic and first seven abdominal spiracles open, notwithstanding numerous statements to the contrary. The last pair of abdominal spiracles are non-functional as nearly as I can judge from preserved specimens. The early instars are exclusively aquatic although it sometimes happens that the eggs are

laid a short distance from the margin of the water and as a consequence the first instar larva may have a short distance to crawl before it can enter the water. When fully fed, the final instar larva leaves the water to construct a pupal chamber, and in search of a suitable site may wander a considerable distance from the water; and it would appear that it is for use at this time that the functional spiracles are retained.

(3) All larvae of the groups of the Diptera that have pupae which remain beneath the surface and utilise the oxygen dissolved in the water are apneustic, apparently without exception. A few CULICIDAE, SYRPHIDAE, and EPHYDRIDAE which have pupae that remain beneath the surface and in which the pupae or puparia pierce the air spaces of aquatic plants, have metapneustic larvae which also pierce the intercellular air spaces. All larvae that pupate at the surface and have pupae that take in air directly from the atmosphere have one or more pairs of functional spiracles, as also have all larvae that leave the water for pupation (TIPULIDAE, TABANIDAE, SYRPHIDAE, etc.). The aquatic TIPULIDAE pupate at the surface or emerge from the water before pupation. Only a single exception, *Antocha*, appears to be known. *Antocha* pupates beneath the surface, and its pupae possess cuticular gills. *Antocha* larvae are apneustic, whereas those of all other aquatic TIPULIDAE possess functional spiracles. *Antocha* and *Chaoborus* are a case of parallel adaptation in two genera of different families. *Chaoborus* larvae are apneustic, and, like their propneustic pupae, remain beneath the surface of the water, whereas in the vast majority of the CULICIDAE both larvae and pupae rise to the surface to take in oxygen directly from the atmosphere.

(4) The EPHYDRIDAE of the genera *Notiphila* and *Hydrellia*, which have the postabdominal spiracles modified to tap the intercellular air spaces of aquatic plants, are of particular interest. They differ from the vast majority of the Cyclorrhapha in being metapneustic in all three instars instead of amphipneustic in the second and third instars. As these EPHYDRIDAE are among the few aquatic cyclorrhaphous larvae which do not emerge from the water to pupate, it seems likely that owing to a change in habits the prothoracic spiracles have had no selective value and as a consequence have become non-functional. This hypothesis is supported by the fact that in a very different cyclorrhaphous larva, the Syrphid *Chrysogaster*, which has similar root-piercing habits (Varley, 1937), the prothoracic spiracles have also become non-functional.

(5) Except for one terrestrial genus (*Eneoclya*) of the family LIMNOPHILIDAE, all the larvae of the Trichoptera remain beneath the surface of the water where they also pupate, and none have functional spiracles. There can be little doubt that *Eneoclya* is secondarily terrestrial, not primitively so, and that it is derived from an apneustic strictly aquatic group of the LIMNOPHILIDAE. According to some writers (e.g. Berlese, 1909), the spiracles are functional, but from the work of Lübben (1907, p. 84) it is certain that the terrestrial *Eneoclya* is also apneustic, which is to be expected on the general grounds that characters once lost are not often reacquired (Dollo's Law). Keilin (1944) has recently described an exactly parallel instance in the Diptera, where the terrestrial but

apneustic *Forcipomyia* is derived from the apneustic aquatic CERATOPOGONIDAE.

(6) In a large number of aquatic beetles (GYRINIDAE, HYGROBIIDAE, HALIPLIDAE, ELMIDAE, LIMNICHIDAE, at least some PTILODACTYLIDAE, some PSEPHENIDAE, and the Berosini among the HYDROPHILIDAE) the first instars are always apneustic and remain beneath the surface of the water. The early instars of some groups extract the dissolved oxygen from the water by means of abdominal or anal tracheal gills or the thinner parts of the body cuticle. The final instar larvae, in addition to possessing the abdominal or anal gills of the earlier instars, also have one or more pairs of functional spiracles. When fully fed these larvae invariably emerge from the water to construct pupal cells or cocoons, and it is reasonable to suppose that it is for use at this time that at least some of the functional spiracles are retained. The only known aquatic coleopterous larva which is apneustic in its final instar is *Psephenoides*, and *Psephenoides* is the only known beetle larvae which pupates beneath the water in such a fashion that the water is actually in contact with the pupa.

(7) In the DYTISCIDAE, AMPHIZOIDAE, CHRYSOMELIDAE (Donacini), and probably also in *Noterus* (NOTERIDAE), the first and intermediate instars have only the postabdominal spiracles functional. In the DYTISCIDAE and AMPHIZOIDAE, the young larvae rise to the surface of the water in order to take in air through their postabdominal spiracles. Although the third instar of both of these families is peripneustic, it is very interesting to note that, judging from the habits of the DYTISCIDAE, only the postabdominal spiracles are used while in the water. The reason for the exclusive use of this pair of spiracles would appear to lie in the fact that the centre of gravity of the larva is in the thoracic region and that when suspended from the surface film by its cerci, the larva is in the best possible position to make a quick descent if attacked. Furthermore, the presence of apical cerci which can be used for holding the larva to the surface layer provides ready to hand a method of suspension not available near any other spiracle-bearing segment. In short, we may assume that the apical pair of abdominal spiracles is selected for taking in air at the surface because the use of this particular pair of spiracles for this purpose involves the minimum structural alteration from the primitive form and places the larva in the best possible position to make a quick escape from the surface if attacked. In many DYTISCIDAE the postabdominal spiracles, although always capable of functioning, are not often used by the first instar larvae since sufficient oxygen is absorbed through the body cuticle. In the Hydroporini all instars may survive without coming to the surface so long as the water is well aerated. In the third instar of all DYTISCIDAE, the eight anterior pairs of functional spiracles normally function only when the larva emerges from the water in order to pupate.

(8) Although the early instars of *Noterus* are unknown, it seems fairly safe to assume from the mode of respiration of the third instar that the first instar is metapneustic like that of all related families of Adephaga. In the NOTERIDAE and Donacini only the postabdominal spiracles are

functional in the first instars, and in both groups they are modified to form piercing organs which are used to extract air from the tissues of aquatic plants. It is probable that the general body cuticle in both groups plays a more important part in respiration than the post-abdominal spiracles, as is certainly the case in the Hydroporini and some other DYTISCIDAE and as has been proved to be the case in some species of *Donacia* by Hoffman (1940). Although in *Noterus* and the Donacini the postabdominal spiracles may be only of secondary importance in most waters, it is clear that under conditions which considerably reduce the oxygen tension the larvae may have to depend absolutely on these spiracles for survival. The latter part of the third instar of *Noterus* and the Donacini, prior to pupation, is spent in a gas-filled cocoon under water, and it must be for use at this time that the anterior pairs of functional spiracles have been retained in the third instar larvae.

B. Keilin's rules.

In a most interesting paper on the development of the respiratory systems of terrestrial and aquatic dipterous larvae, Keilin (1944, p. 31) has proposed eleven generalisations. I have already (p. 457) commented on the first three of these, which agree with everything I have found in the larvae of the other Holometabola. His generalisations four to eleven deal mainly with the precise details of the sequences of the functional spiracles in the ontogeny of the larvae, and it is of some interest to see if they apply to other orders besides the Diptera. These generalisations may be examined in the order in which they are given by Keilin:—

“(4) The metathoracic spiracles of dipterous larvae, except those of the BIBIONIDAE, remain non-functional in all stages of the larva; however they become functional in adult flies.”

The metathoracic spiracle is nearly always non-functional in holometabolous larvae. Exceptions, in addition to the BIBIONIDAE, are the Siphonaptera (Sikes, 1930). The metathoracic spiracle always appears to be non-functional in pupae, judging from the limited numbers of pupae I have been able to examine of other orders. No pupae of the Zeugloptera or Strepsiptera have been seen by me. The metathoracic spiracle of adult Holometabola is usually functional.

“(5) The polypneustic larvae pass during their development through oligopneustic stages.”

With rare exceptions (Diptera, *Eneocyla*, and a few others), terrestrial insect larvae are polypneustic in all instars. Terrestrial dipterous larvae, endoparasitic dipterous and hymenopterous larvae, and most, but not all, aquatic larvae of other orders which are polypneustic in their final instar, go through oligopneustic instars. The large number of HYDROPHILIDAE which are polypneustic in all instars are a striking exception among aquatic larvae. Keilin's generalisation is true only of aquatic and endoparasitic larvae. It applies to all Diptera only because the common ancestor of these lived in a liquid or semi-liquid medium. It applies to no other order, but only to some aquatic and endoparasitic larvae of other orders.

"(6) The mesothoracic spiracles together with their tracheal metameres are absent in all larval stages."

In pterygote larvae mesothoracic spiracles are present in all but a few orders—*e.g.*, Mecoptera, Siphonaptera, Diptera, Lepidoptera, some Hymenoptera, and some specialised Coleoptera, which have prothoracic spiracles. Mesothoracic and prothoracic spiracles exclude each other (except in a few Apterygota) as first shown by Palmén (1877). From the distribution of the first thoracic spiracle among the various pterygote orders, it seems certain that its presence on the mesothorax represents a more primitive condition than its presence on the prothorax. All of the holometabolous orders which have the first thoracic spiracle on the prothorax may be derived from ancestors not very unlike the recent orders which have the first spiracle on the mesothorax. From the distribution of the first thoracic spiracle it would appear that the prothoracic spiracle of the Lepidoptera, Diptera, and others is, in point of fact, the mesothoracic spiracle which has migrated on to the prothorax. This view is held by Snodgrass (1935). The summary of the embryology of the Lepidoptera, Diptera, and Siphonaptera given by Johannsen and Butt (1941) shows that in these three orders the mesothoracic spiracle migrates to its position on the prothorax in later embryos. Thus it is the prothoracic, not the mesothoracic, tracheo-spiracular metamere which has been lost.

"(7) There are no transition stages between the oligopneustic and polypneustic systems during the development of the larva. The seven pairs of abdominal spiracles are either all functional or all closed."

In some aquatic beetle (GYRINIDAE) and moth (some *Nymphula* spp.) larvae, some endoparasitic hymenopterous larvae, and many Hemiptera, only the first three to six abdominal spiracles are functional.

"(8) The metapneustic system appears as the first stage of development in all respiratory systems except the apneustic one."

In the Holometabola, this is true only of the Diptera, some aquatic Coleoptera, and a few endoparasitic Hymenoptera. A metapneustic first instar is an adaptation to life in fluids, and its common occurrence in the Diptera is further evidence that the archetype of the Diptera had a larva that lived in fluids.

"(9) The fact that the metapneustic system occurs also in the development of the hemipneustic system is of special interest. The appearance of a pair of postabdominal functional spiracles for a short period in mycetophylid larvae shows first of all that the hemipneustic respiratory system derives from the peripneustic system. It shows also that the closed non-functional spiracle ought not to be considered as a primitive rudiment of an organ in development but as a secondary rudimentary form of organ derived phylogenetically from a normal functional spiracle."

A number of aquatic larvae of other orders which have a hemipneustic final instar have apneustic early instars—*e.g.*, some Megaloptera (*Sialis*) and some Coleoptera (HYGROBIIDAE, HALIPLIDAE). Some endoparasitic Hymenoptera with hemipneustic final instars also have apneustic early instars (Clausen, 1940). Among terrestrial larvae, some

CHRYSOMELIDAE (*Timarcha*, and possibly some CASSIDINAE) and many MELOIDAE have hemipneustic instars which are not preceded by metapneustic instars. Reduction in the number of functional spiracles occurs in some seed-infesting weevils—e.g., many APIONINAE are hemipneustic. So little information and material are available of seed-infesting CURCULIONIDAE that I have left them out. My use of the term “terrestrial” excludes seed-infesting weevils.

“(10) The development of the hemipneustic system differs from that of other polypneustic systems by passing through a propneustic stage.”

In at least some SIALIDAE and in the HYGROBIIDAE and HALIPLIDAE the hemipneustic final instar is preceded by apneustic early instars. The terrestrial hemipneustic CHRYSOMELIDAE (*Timarcha* and probably some CASSIDINAE) and MELOIDAE do not pass through propneustic instars nor do some hemipneustic endoparasitic Hymenoptera.

“(11) In the course of development of different respiratory systems, the functional spiracles appear in the order of their morphological and physiological importance. If the relative importance of spiracles in a peripneustic system can be expressed as $S_8 > S_1 > S_{1-7}$, the successive stages of development are: metapneustic, amphipneustic and peripneustic. The only exception to this rule is the appearance, for only a very short period, of a postabdominal spiracle in the development of hemipneustic larvae of mycetophilids.”

Among terrestrial larvae, the development sequence metapneustic→amphipneustic→peripneustic occurs only in a few orthorrhaphous Diptera (SCATOPSIDAE). Table 1 shows clearly that among aquatic larvae the developmental sequence metapneustic→amphipneustic→peripneustic is unknown. The most usual developmental sequence is apneustic→peripneustic for both aquatic and endoparasitic holometabolous larvae, but metapneustic→peripneustic sequences without the intervention of an amphipneustic instar commonly occur.

From the foregoing remarks it will be evident that: (1) Keilin's generalisations five and seven to eleven have only a very limited validity as they are true only of a single highly specialised order of insects; and (2) his sixth generalisation does not agree in any way with the facts.

The distinction between polypneustic and oligopneustic respiratory systems breaks down to a considerable extent when all groups of insects are considered, particularly in view of the presence of only six pairs of functional abdominal spiracles in the larvae of many Heteroptera.

C. Reduction of spiracles in the aquatic larvae of the Hemimetabola.

Apart from a very few Orthoptera (ACRIDIDAE, TETRIGIDAE), which are amphibious rather than strictly aquatic, the aquatic Hemimetabola belong to the orders Odonata, Plecoptera, Hemiptera, and Ephemeroptera, but relatively few Hemiptera are aquatic.

From specimens examined by myself and various accounts (Dewitz, 1890; Portier, 1911; Tillyard, 1917; etc.) of the tracheal system of the Odonata, it is clear that the abdominal spiracles are non-functional throughout the larval instars. In the AESHNIDAE, the two mesothoracic spiracles are functional only in the final instar. In the LIBEL-

LULIDAE they⁸ are functional in both the final and intermediate instars, but it appears that they may be non-functional in the first instar. In the AGRIONIDAE, the mesothoracic spiracles are open in the final and, according to accounts, intermediate instars, but I have not been able to find a definite statement of their condition in the first instar. All Odonata leave the water to shed their last larval cuticle, and they often crawl several feet away either on an object projecting out of the water or they may crawl a short distance on land in order to find a suitable object on which to climb. Before ecdysis they usually rest a short time apparently in order to dry themselves thoroughly. And it may be supposed that it is for use at this time that the first pair of thoracic spiracles is retained in a functional condition. Tillyard has shown that the larvae of some Aeshnids leave the water at night to hunt over stones near the water. Many of the larvae both in their final and intermediate instars will rise to the surface of poorly aerated water in order to hold their spiracles above the surface (AESHNIDAE, LIBELLULIDAE); and in this connection it is interesting to note the unusual displacement towards the dorsum of the first pair of thoracic spiracles in the AESHNIDAE, LIBELLULIDAE, and AGRIONIDAE.

It is generally claimed that the Plecoptera are apneustic. All young larvae I have been able to examine are certainly apneustic, but larvae, apparently in their final instar, of *Eusthenia* and several unidentified South American species have the two pairs of thoracic spiracles functional. In the case of *Eusthenia* I am not certain that the first seven abdominal spiracles are incapable of taking in air. As a rule, the final instar cuticle is shed fairly near the water, usually on a stone partly submerged in the stream.

All larval instars of the Ephemeroptera are apneustic, and it is interesting to note that they frequently shed the last larval skin at the surface, sometimes even in swiftly running water, or actually beneath the surface. When the last larval cuticle is shed beneath the surface, it is, of course, the first imaginal instar (pupa, subimago) which escapes from the water. Some final instar mayfly larvae crawl out of the water to shed their cuticle, but they rarely, so far as I can discover, crawl any distance (the North American *Siphonurus* may crawl up to three to four inches out of the water) from the water as often do the Odonata.

The above account shows that it is probable that the generalisations based on the developmental sequences of functional spiracles in holometabolous larvae apply equally well to the larvae of the Odonata, Plecoptera, and Ephemeroptera. If the first instar larvae of the LIBELLULIDAE and AESHNIDAE prove to be apneustic, the ontogenetic sequences will be similar to those of the cyclorrhaphous Diptera, most of which increase their number of functional spiracles in an intermediate instar. For various reasons I have neglected the aquatic Hemiptera, but descriptions of the functional spiracles of the BELOSTOMATIDAE,

⁸ It seems probable, judging from size and position, that the metathoracic pair may always be non-functional in the LIBELLULIDAE, AGRIONIDAE, and other families in instars which possess functional mesothoracic spiracles. In all specimens of the three families which I have been able to examine, the metathoracic spiracles were always non-functional.

NEPIDAE, and a few others show that the sequences of functional spiracles in the Hemiptera also agree with my generalisations.

D. Ecological and other considerations.

Until now I have been concerned with formulating generalisations which will apply to the respiratory systems of the aquatic larvae of all insects and with an examination of Keilin's rules based on a study of the development of the respiratory system in various Diptera. From Table 1 and the discussion immediately following, it is fairly evident that when, owing to a change in habits, functional spiracles no longer play a significant part in the respiration of a particular instar they sooner or later become non-functional. In other words, there may be an intimate relation between the habits of a larva and the structure of its respiratory system. Among the different kinds of environments there are only two which considerably affect the use of spiracles in larvae, namely, the endoparasitic and aquatic. The vast majority of endoparasitic larvae belong to the Hymenoptera and Diptera. The endoparasitic Diptera bear the unmistakable stamp of being descended from liquid inhabiting ancestors. Their ontogenetic sequences of functional spiracles were clearly fixed before they acquired parasitic habits, and with few exceptions have not since been altered.⁹

It has been established that the number of functional spiracles is intimately related to the medium in which the larva lives; and in all aquatic larvae the number of functional spiracles remains the same or increases, but never decreases, in the successive larval instars. The invasion of water has made possible new methods of respiration and as a consequence decreased in varying degree the dependence of the larva on taking in oxygen directly from the atmosphere. In each instar the number of functional spiracles is directly related to the degree to which that instar is dependent on atmospheric oxygen or on tapping the inter-cellular air-spaces of aquatic plants. The direct dependence on atmospheric oxygen of all aquatic larvae remains the same or increases, but never decreases, throughout larval life. And it is this biological fact that makes it possible to generalise about the developmental sequences of the functional spiracles.

Nearly all aquatic larvae lay their eggs in the water, on its surface, or on stems, leaves, and other objects overhanging the water. On

⁹ In this paper I have continually stressed the fact that the ontogenetic sequences of functional spiracles in the larvae of recent Diptera clearly show that they are descended from an ancestor that lived as a larva in liquids. But the ancestral dipterous larva could hardly have been aquatic, since among recent insects there is not a single instance of a larva losing its legs after it has become aquatic; and the complete absence of legs in the Order is one of its most conspicuous features. I believe that the prototype of the Diptera had a larva which lived in liquid or semi-liquid decaying vegetable matter, possibly fungi. In this connection it is of interest to note that all the aquatic HYDROPHILIDAE have well-developed legs but among the *secondarily* terrestrial SPHAERIDIINAE, which live in decaying vegetation and cow dung, the legs are much reduced or absent.

In this and a recent paper on pupae (1946, *Proc. zool. Soc. Lond.* 116 : 282-328, 64 figs.) the classification which divides the Diptera into the suborders Orthorrhapha and Cyclorrhapha is used. I now consider that this classification is phylogenetically unsound. The division of the Diptera into Nematocera and Brachycera agrees more closely with the facts of their phylogeny. In such a classification the Brachycera are at present divided into two series, the Brachycera-Orthorrhapha and the Brachycera-Cyclorrhapha.

hatching the larvae that are not already in the water drop into it directly. There are, however, a number of exceptions. For instance, *Sialis* and a number of Trichoptera sometimes lay eggs on objects some distance from the water. In such cases the newly hatched larvae have to make their way to the water, and to this end all their first efforts are directed. The larvae of *Sialis* and the Trichoptera are apneustic and do not feed before entering the water. In these forms there is no question of the first instar larva having an established pre-aquatic phase in the sense that the final instar of many groups has a well-marked, terrestrial, post-aquatic phase which is obligatory before pupation. In some peripneustic HYDROPHILIDAE the first instar larvae may remain up to twenty-four hours in their gas-filled egg-cocoon before breaking into the water, but during this period they do not feed. A number of CULICIDAE lay their eggs in places which are dry at the time but will subsequently have water. According to accounts, the eggs of such species do not hatch simultaneously, but some of the eggs of each batch must be wetted more than once before they will hatch—a mechanism which tends to prevent the death of all larvae before it has rained sufficiently to provide the quantity of water necessary for larval development. The eggs of some arctic and alpine species are laid where there is no water, and these eggs hatch only when there is a thaw which provides the larvae with water. When hatched, however, these Culicid larvae cannot withstand drying for any appreciable period.

Once having entered the water, the larvae of all Holometabola remain there¹⁰ until the final instar. The final instar larva may pupate in the water or it may emerge to pupate above the water. Since the intermediate instars, like the first instar, remain for the whole of their existence in the water, they would be expected to have the same number of functional spiracles as the first instar, which is nearly always the case (Table 1). The larvae of many groups emerge for pupation near the end of their final instar, and, as out of the water they are not able to make use of any alternative methods of respiration acquired for life in the water, it is only to be expected that in the final instar the primitive peripneustic system should often be less reduced and certainly never more reduced than in the preceding instars. Owing to the fact that the number of functional spiracles can only be changed at ecdysis, the additional spiracles, if any, of the third (final) instar are present throughout the aquatic phase of this instar, when they can scarcely be of use.

Certain physical and climatic factors may sometimes be of secondary importance in preserving a greater number of functional spiracles in the final instar than in those preceding. For instance, the relation of surface area to volume is most favourable for the cutaneous extraction of dissolved oxygen from the water when the larva is smallest and thereafter becomes continuously less favourable, being least favourable in the final instar larva. In this connection the development of the gills in some

¹⁰ Some of the peripneustic HYDROPHILIDAE may be found to be exceptional in this respect. Many HYDROPHILIDAE and some others—e.g., eristaline Syrphids—are able to survive when ponds lose their free water providing the soil does not get too dry. As previously mentioned, *Archichauliodes* leaves the water for a short time at each ecdysis.

apneustic lepidopterous larvae (*Nymphula* spp.) is most instructive. In the first instar there are no gills. In the second instar gills, which are no more than simple extensions of the body wall containing tracheae, are acquired. At each subsequent moult further gills are acquired, so that as the larva grows the favourable relation of surface area to volume is more or less maintained.

Another circumstance that may, perhaps, affect the number of functional spiracles is the fact that a very large number, if not the majority, of aquatic larvae inhabit the more numerous smaller bodies of standing water and the smaller streams. These aquatic larvae must often experience the drying up of the small ponds and streams in which they are living. The chance of the water in temporary ponds and streams drying up during early larval life is for any particular species much less on the average than the chances of the water drying up during the later larval instars.

E. Reduction of spiracles in endoparasitic larvae.

The subject of the reduction of functional spiracles in aquatic larvae can hardly be left without noting some interesting cases of parallel structural modifications in endoparasitic larvae. As previously stated, the vast majority of endoparasitic larvae belong to the Diptera and Hymenoptera. The endoparasitic Diptera are nearly all cyclorrhaphous forms which are metapneustic in their first instar and amphipneustic in subsequent instars and which are obviously descended from aquatic ancestors. Their number of functional spiracles was already so reduced by the time they became parasitic that little possibility existed of further variation, since spiracles that become non-functional remain so, as is strikingly demonstrated by the genera *Enoecyla* and *Forcipomyia* previously mentioned.

In the endoparasitic Hymenoptera the first instar is usually apneustic but sometimes metapneustic, whereas the final instar is nearly always peripneustic.¹¹ The ontogenetic sequences of functional spiracles is thus the same as in many groups of aquatic larvae; and the generalisations given on p. 459 apply equally well except for the fourth. In endoparasitic Hymenoptera which have more than three instars it often but not always happens that a peripneustic system is retained in the penultimate instar, so that these larvae are similar to the Cyclorrhapha in that a change in the number of functional spiracles occurs in an intermediate instar.

The similarity in the reduction of functional spiracles in aquatic larvae and those of the endoparasitic Hymenoptera is due to a fundamental similarity in some directions of life in the water and life in the fluids of the hosts of the Hymenoptera. The primitive number of spiracles is retained in the later instars of the Hymenoptera presumably because they must be able to take oxygen directly from the atmosphere owing to the usual drying up of the host fluids at about the time the larva is mature or because the mature or nearly mature larva emerges from the host before pupation. The three principal methods of respira-

¹¹ A summary of the distribution of functional spiracles in hymenopterous larvae is contained in Clausen (1940).

tion developed by endoparasitic larvae are remarkably similar to those developed by aquatic larvae. By one means or another, many endoparasites establish direct communication with the atmosphere; and these may be compared with the numerous aquatic larvae that have to come to the surface to take in oxygen. Many endoparasites pierce the tracheae of their hosts; and these may be compared to the relatively few aquatic larvae which tap the intercellular air-spaces of aquatic plants. Many endoparasites, particularly in their first two instars, depend entirely on cutaneous respiration, as also do many apneustic and spiracle-bearing aquatic larvae. In conclusion, it may be noted that some endoparasites develop "blood" gills as do many aquatic larvae. These blood gills, however, are probably primarily concerned with the extraction of salts from the fluids which bathe them (Wigglesworth, 1939).

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AN ANALYSIS OF CAPTURES OF APHIDIDAE (HEMIPTERA) IN A LIGHT TRAP

BY L. BROADBENT

(Rothamsted Experimental Station, Harpenden, Herts.)

Communicated by Dr. C. B. Williams, M.A.

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WITH 1 GRAPH

SUMMARY.

FOUR years' captures of aphides in a light trap are analysed, on arithmetic and logarithmic bases, month by month and throughout the night. It is shown that aphides were flying during the night in each month from May to November. An attempt is made to correlate the captures of one summer with the various meteorological factors prevailing; activity was positively correlated with the maximum temperature of the previous day and with the evening reading of the dew point; it was negatively correlated with the wind force of the previous afternoon, and wind direction also had a significant effect. Population changes from year to year were probably dependent to a great extent on the summer rainfall, the population being lower in wet years.

INTRODUCTION.

Apart from their economic importance as pests, aphides play the most important part in disseminating plant virus diseases. As only moving aphides can act as vectors their movements and the conditions under which alatae fly are of great interest; many observations have been made in the laboratory and in the field, and optimum conditions for aphid flight have been postulated. Different workers are not in complete agreement on this subject and field studies have shown that the extent of existing knowledge is inadequate, since aphides are found in the air under conditions very different from the optimum.

In a light trap operated at Rothamsted Experimental Station from 1933 to 1937 Dr. C. B. Williams caught numerous aphides. Since an analysis of these data, and of the meteorological conditions prevailing, might be of value, Dr. Williams kindly placed his original data at the writer's disposal for this purpose.

THE TRAP.

The data were obtained at Rothamsted Experimental Station during the four years 1933-1936, using a light trap. Full details of the trap have been published (Williams, 1935). The trap was placed on the edge of one of the experimental fields, about 400 feet above sea level and about 3 ft. 6 in. from the ground. It was on the western edge of a field under mangolds each year, and about four yards from the south-west corner

of a small orchard (about forty low trees). To the west and north were pasture and parkland, with many hedgerow trees, while 100 yards to the north-east and east was a large area of allotments.

The period of night was assumed to start half an hour after sunset and to end half an hour before sunrise. The intervening time was divided into eight equal parts, the length of which varied from week to week according to the length of the night. A clockwork mechanism operated a series of eight bottles so that the catches in the different periods could be separated. It is likely that the different species react to external conditions in different ways, although aphides as a family are morphologically very similar. However, data are available only for total catches of aphides; and the results of the analysis are of general application only.

TOTAL CATCHES IN THE DIFFERENT YEARS.

No aphides were caught before May or after November in any year. Table 1 gives the total catches for the different months in the four years and the annual totals.

TABLE 1.
Total number of aphides caught.

	May	June	July	Aug.	Sept.	Oct.	Nov.	Total
1933	9	73	884	654	255	71	0	1,946
1934	0	35	164	28	240	7	0	474
1935	7	73	86	438	20	9	2	641
1936	0	28	12	34	253	21	1	349
Four-year Total ...								3,410

The total catches have been reduced to the arithmetic and geometric means of daily catches in Table 2. As Williams (1935, 1936) pointed

TABLE 2.
Means of daily catches in each month.

ARITHMETIC MEANS								
	May	June	July	Aug.	Sept.	Oct.	Nov.	
1933	0.29	2.43	28.50	21.10	8.50	2.29	0.00	
1934	0.00	1.17	5.29	0.90	8.00	0.23	0.00	
1935	0.23	2.43	2.77	14.13	0.87	0.29	0.07	
1936	0.00	1.47	0.39	1.10	8.43	0.68	0.03	
Mean of 4 years	0.13	1.88	9.24	9.31	6.45	0.87	0.03	
GEOMETRIC MEANS								
1933	0.17	1.54	5.89	10.25	2.19	0.77	0.00	
1934	0.00	0.53	2.14	0.44	0.97	0.11	0.00	
1935	0.13	0.79	0.96	4.52	0.50	0.16	0.05	
1936	0.00	0.83	0.27	0.41	2.67	0.34	0.02	
Mean of 4 years	0.08	0.92	2.32	3.91	1.58	0.35	0.02	

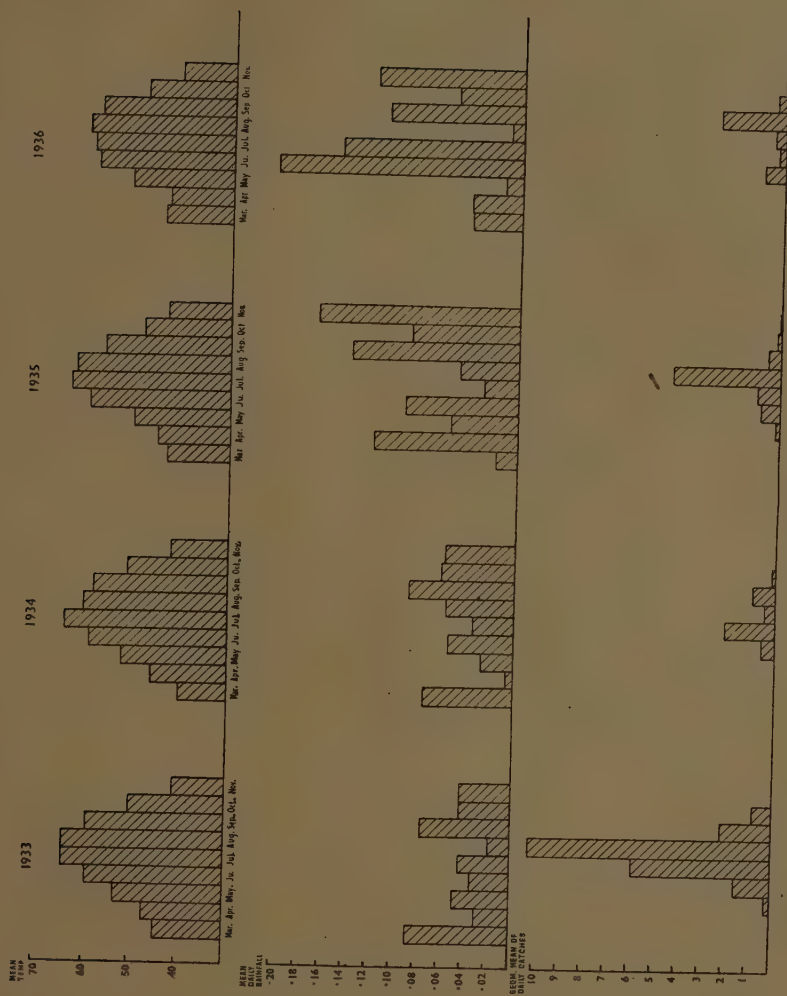


Fig. 1.
Geometric means of daily catches, mean temperature and mean daily rainfall in each month.

out, arithmetic means give misleading results for data such as these, and geometric means (the arithmetic mean of the $\log(n+1)$ catches = the logarithm of the geometric mean) are used in the following analysis. The highest mean catch occurred in August in 1933, in July in 1934, in August in 1935 and in September in 1936. Thomas and Vevai (1940), in North Wales, found few aphides before June or after July in the years 1935-1936; thus the peak of aphid numbers varied considerably from one part of the country to another, as well as from year to year.

The annual and monthly totals probably reflect population changes rather than variation in activity, which is reflected in the daily catches. In fig. 1 the geometric mean daily catch is given for each month in each year, together with the mean temperature and mean rainfall. The temperature curve is similar in each year, with 1933 slightly higher than the others. The rainfall, however, fluctuates greatly from month to month and from year to year; 1933 was generally dry and the catch was extremely high. The spring of 1934 was drier than that of 1933, but the summer was wetter. The highest catch occurred in the driest month, *i.e.*, July. The spring of 1935 was very wet, but July and August were relatively dry, and the catch rose sharply in August. In 1936 a very wet summer followed a dry spring. August, however, was exceptionally dry and the catch rose to a low peak in September. Thus it would appear that in these four years the most important weather factor affecting the population of aphides, at least of *alatae*, was the rainfall in the summer months. Williams (1940) came to the same conclusion regarding the total catches of insects.

Although the weather conditions of 1934 did not differ very greatly from those of 1933, the catches were much less. This might have been caused by the activities of predators and parasites, which are often (though by no means always) more numerous than usual after a year of high numbers of aphides, so that the aphid population in that year is checked. The only data on parasites and predators available from the light trap records is for the Lacewings (Neuroptera), and these support the above suggestion, the numbers being:

1933	...	45	1934	...	121
1935	...	75	1936	...	5

TABLE 3.

Distribution of nights with no catch and with high catches in the four years.

Number of nights with captures of insects, 1st June—31st Oct.	0	50-100	Over 100
1933	46	4	6
1934	95	1	1
1935	84	1	1
1936	88	0	1

The number of nights in each of the four seasons from June to October with no catch, with catches between 50 and 100, and with catches over 100 is shown in Table 3. The highest catch recorded was 207 on the night of 26th July, 1933. Since the number of nights with

no catch is high in the three years 1934-36 all attempts to correlate catch with weather conditions have been made with the data obtained for the four months June to September, 1933, during which time 25 out of a total of 120 nights gave no catch.

THE HOURS OF ACTIVITY DURING THE NIGHT.

Table 4 shows the distribution of the catches between the eight periods of the night for the four years. It will be seen that most aphides were caught in period 1 in 1934 and 1936, in period 2 in 1933 and in period 3 in 1935. The minimum catches were in period 6 in 1936, in period 7 in 1934 and 1935, and in period 8 in 1933. The average for the four years gives the maximum in period 1 and the minimum in period 7. The minimum catch was 30 per cent. of the maximum.

On the logarithmic basis the maximum catch was in the first period in all four years, the minimum catch in periods 5 and 6 in 1936, in period 6 in 1935 and in period 7 in 1933 and 1934. The four years combined give the maximum catch in the first period and the minimum in the 7th. The minimum catch was 34 per cent. of the maximum.

TABLE 4.

Distribution of APHIDIDAE in the eight periods of the night for each year and for all four years combined ; on number and log. basis.

Year	No. of nights	Period of night							
		1	2	3	4	5	6	7	8
		Sum of numbers							
1933	214	317	323	279	223	219	304	145	136
1934	214	184	67	47	34	41	40	24	37
1935	214	106	113	116	97	63	47	44	55
1936	191	161	48	62	26	9	8	19	16
Total	833	768	551	504	380	332	399	232	244
Mean per night		0.92	0.66	0.61	0.46	0.40	0.48	0.28	0.29
		Sum of log. (n + 1)							
1933		44.47	33.78	31.52	30.01	28.59	29.11	18.76	20.56
1934		10.46	9.43	9.95	7.65	8.08	7.15	4.62	8.08
1935		19.83	17.56	15.38	12.27	11.77	6.62	8.00	7.50
1936		16.04	9.86	9.22	6.90	2.28	2.28	4.60	4.14
Total	...	90.80	70.63	66.07	56.83	50.72	45.16	35.98	40.28
Mean log./night		1.090	0.848	0.793	0.682	0.609	0.542	0.432	0.484
Geometric mean per night		0.29	0.22	0.20	0.17	0.15	0.13	0.10	0.12

Table 5 gives the distribution on a monthly basis for the four years, expressed as percentages of the total catch for the night. In May, June, September and October a large percentage (over 40 per cent. in

each month) of the catch occurred in period 1. In July and August the maximum catch was in period 2 (about 17 per cent. in each month) and the catches were more evenly distributed throughout the night.

TABLE 5.

Percentage of night's total catch during each period of the night in each month ; average of four years.

	Period of night							
	1	2	3	4	5	6	7	8
May	68.8	0.0	25.0	6.2	0.0	0.0	0.0	0.0
June	40.8	17.2	15.3	6.7	2.9	5.7	3.3	8.1
July	12.1	17.4	17.1	12.5	11.6	17.1	6.4	5.8
August	10.2	17.2	16.8	13.7	11.1	11.2	9.2	11.1
Septemb'r	47.8	11.2	10.1	6.9	7.1	7.1	5.8	4.0
October	40.7	28.7	5.6	8.3	8.3	6.6	0.9	0.9

On some nights there was a pronounced increase in catch towards the middle or the end of the night. A few examples are given below :

	Period	1	2	3	4	5	6	7	8
1933									
July 2	...	0	9	7	7	18	95	22	10
" 3	...	0	14	5	7	13	17	6	1
" 17	...	0	0	0	4	5	12	10	5
Aug. 6	...	8	2	4	9	21	27	20	20
" 8	...	0	17	24	26	5	28	10	21
Sept. 1	...	24	1	4	11	31	37	22	9

There was no apparent marked change in meteorological conditions during the different periods of these nights ; on the average the minimum temperatures were above normal, the wind speed below (being dead calm on four of the six nights) and the dew point above normal. The pressure at midnight was rising on three nights and steady on the others.

COMPARISON OF NIGHTS WITH HIGH AND LOW CATCHES.

Table 6 shows the meteorological data for eight nights with high catches and eight nights with low catches. The meteorological records used (except for wind) were obtained at the Rothamsted Meteorological Station, 300 yards to the south of the trap.

The differences between the means of these records for nights of high and low catches are small, but indicate that nights with high catches had higher temperatures, and followed days with slightly higher temperatures ; had less temperature range ; were less windy and followed calmer days ; were less sunny. All the days chosen were rainless, except one, which was followed by a high catch, when it rained for a short period during the day. There was no difference between the two groups in barometric pressure, depression of wet bulb temperature, or dew point and relative humidity at 15 hrs. The relative humidity and dew point at 21 hrs. however, were higher on the nights of high catch.

TABLE 6.
Comparison of weather factors for nights with high and low catches.

1933		High Catches										Low catches										High mean— low mean
		2/7	22/7	23/7	26/7	2/8	6/8	14/8	1/9	Mean	30/6	24/7	25/7	27/7	31/7	5/8	13/8	4/9	Mean			
Catch	...	168	111	119	207	68	111	58	139	123	0	5	7	4	0	6	3	5	4	119		
Log catch—departure from 21-day mean		+1.55	+1.25	+1.19	+1.29	+0.76	+1.08	+0.01	+1.11	+1.14	-0.68	-0.18	-0.13	-0.42	-1.23	-0.20	-0.27	-0.19	-0.41			
Maximum temperature ... ° F.		73.9	76.4	78.3	83.2	79.2	88.3	71.4	69.9	77.6	67.0	80.5	79.1	89.3	62.1	79.7	73.1	76.7	75.9	+1.7		
Minimum temperature ... ° F.		55.3	55.6	55.4	61.5	65.3	61.2	57.5	57.3	58.6	48.2	55.6	52.8	51.3	56.3	57.0	53.5	54.0	53.5	+5.1		
Daily range of temperature ... ° F.		18.6	20.8	22.9	21.7	13.9	27.1	13.9	12.6	19.0	18.8	24.9	26.8	38.0	5.8	22.7	19.6	22.7	22.4	-3.4		
Night wind group		1	1	1	1	3	1	2	2	1.5	1	1	1	4	5	1	2	2	2.1	-0.6		
Day wind group (3-2 hours before sunset)		3	1	3	1	4	3	1	4	2.5	3	3	1	3	5	4	5	4	3.5	-1.0		
Sun, hours		12.2	8.0	9.1	13.9	8.0	10.5	0.6	2.6	8.1	9.9	13.2	12.6	10.0	1.4	9.9	10.1	7.6	9.3	-1.2		
Rain in.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
Barometer (midnight)		30.5	30.2	30.3	30.1	30.5	30.2	30.0	30.2	30.3	30.2	30.2	30.1	30.0	30.0	30.3	30.3	30.4	30.2	+0.1		
Rel. humidity, 15 hours		53	45	47	38	45	35	75	76	51.8	54	46	45	49	71	48	40	57	51.3	+0.5		
Rel. humidity, 21 hours		76	73	73	70	73	64	88	93	76.3	72	65	60	72	69	85	80	83	73.3	+3.0		
Depression of wet bulb, 15 hours ...		10.1	12.9	13.0	16.6	13.2	18.9	5.0	4.8	11.8	9.0	13.5	13.6	12.9	5.2	12.5	13.5	9.7	11.2	+0.6		
Depression of wet bulb, 21 hours ...		4.5	5.0	5.4	6.1	5.3	8.0	2.0	1.1	4.7	4.7	6.9	8.5	5.6	5.4	2.9	3.2	2.8	5.0	-0.3		
Dew point, 15 hours		54	53	56	53	54	51	58	61	55.0	49	57	55	60	53	58	46	58	54.5	-0.5		
Dew point, 21 hours		57	56	58	59	62	61	59	62	59.3	48	56	56	60	50	61	52	56	54.9	+4.4		

ANALYSES OF THE INFLUENCES OF METEOROLOGICAL FACTORS

In the first instance the regression co-efficient of log. catch on each factor was calculated separately. This gives a measure of the effect of the factor when considered alone, without the elimination of other weather factors. Since the meteorological factors are inter-related, this method may show one to have a significant effect, whereas in reality the effect is due entirely to another. To overcome this difficulty the factors which appeared significant when considered singly were later considered in pairs or groups by the method of analysis of variance.

All the data were collected from 3rd June to 30th September, 1933 (120 days). In order to distinguish the daily variations (*i.e.*, activity) from population changes occurring over a longer period, the departure of the log. catch from a 21-day running mean (*i.e.*, the mean of the appropriate day and of the ten days before and after it) of the log. catches has been used. While it is possible that the regressions in some instances might not be truly linear, to simplify the calculations linear regressions have been assumed throughout.

TEMPERATURE.

In the summer of 1933 there were heat waves in each month, followed by periods of relatively low temperatures and the trend from month to month was obscured by these fluctuations. It was decided that this slight change from month to month could be neglected and that regressions of the departures of the log. catch against actual temperatures would be permissible. Minimum temperature had a regression co-efficient of $+0.038 \pm 0.011$, significant at 0.1 per cent.; maximum temperature of the previous day had a co-efficient of $+0.035 \pm 0.006$, significant at 0.1 per cent.

Maximum and minimum temperatures are positively correlated, that is a high night temperature is likely to follow a high day temperature. When the two temperatures were considered in conjunction an analysis of variance showed that the maximum temperature of the previous day apparently had much more effect on the catch than the minimum temperature of the night. Obviously, however, the minimum temperature of the night must have had a limiting effect in determining whether or not the insects could remain in the air. Wellington (1945) noticed that any insect cooled below its minimum flight temperature invariably folded its wings in the normal rest position; it may be presumed, therefore, that the temperatures of the layers of air in which the aphides were flying were above this critical temperature. This temperature may well vary for different species, as well may the other factors influencing flight. The lowest minimum temperature when aphides were trapped in the later periods of the night was 47° F. Aphides were caught in the earlier periods of nights, which later reached minima as low as 43° F.

HUMIDITY.

Regression of log. catch on relative humidity, dew point (a measure of absolute humidity) and the depression of the wet bulb thermometer

(a measure of evaporation), all read at 15 hrs. and 21 hrs. on the day before the catch, gave results as follows :

	Regression coefficient	Significant at
Relative humidity, 1500 hrs.	-0.007 ± 0.003	5%
" " 2100 hrs.	-0.011 ± 0.005	5%
Dew point, 1500 hrs.	$+0.029 \pm 0.009$	1%
" " 2100 hrs.	$+0.049 \pm 0.010$	0.1%
Depression of wet bulb, 1500 hrs.	$+0.040 \pm 0.011$	0.1%
" " " 2100 hrs.	$+0.076 \pm 0.022$	0.1%

A regression analysis of log. catch on the two readings of the wet bulb temperature depression showed that each was significant independently, but that the 15 hrs. reading gave a slightly better fit.

Temperature and humidity are highly correlated, so that regression analyses of log. catch on maximum temperature together with the 15 hrs. depression of wet bulb temperature and with the 21 hrs. readings of dew point were made. These showed that the depression of wet bulb had no significant effect when considered in conjunction with maximum temperature, but that dew point had such an effect.

Freeman (1945) stated that : "APHIDIDAE develop the greatest numbers in the aerial fauna under conditions of high humidity." High humidity in this statement refers to the range of relative humidity 60-73 per cent. The range of dew point experienced in 1933 was from 42° to 64° F. Within this range the catch rose steadily with increasing dew point, but, on the other hand, so did the temperatures, as shown by the following figures :

Dew point (° F.), 2100 hrs.	42-49	50-53	54-57	58-64
Number of readings	28	37	34	21
Mean departure of log. catch from mean	-0.21	-0.09	+0.02	+0.47
Mean maximum temperature	66.4	69.1	72.7	76.7
Mean minimum temperature	47.9	51.7	54.7	57.7

In Table 6 the nights with high catches always followed a rise, sometime substantial, in dew point from 15 hrs. to 21 hrs. On the other hand, five of the nights with low catch followed days in which the dew point fell, or remained stationary, between these times. Summing the departures of log. catch from mean in two groups, (i) when the dew point was rising, (ii) when steady or falling, it was found that the mean departure for group (i) was +0.08, and for group (ii) -0.07. It would appear, therefore, that changes in humidity influenced the activity of the aphides.

RAIN.

Rain fell during 26 afternoons and during 25 nights in the period under consideration. "Days" in the following table refer to the period from noon until sunset. Days with rain only in the morning have not been included.

	Mean log. catch	Mean departure of log. catch from mean
94 days without rain	0.82	+0.091
26 days with rain	0.84	-0.275
95 nights without rain	0.82	+0.073
25 nights with rain	0.83	-0.275
8 days with rain followed by nights with rain	0.83	-0.420

It would appear that rain during the afternoon, the night, or both, considerably reduced the catch. On the other hand, a consideration of other factors makes it possible that this apparent effect is unreal. The average wind speed on days without rain was Group 4 (5-10 m.p.h.), the same as on days with rain during the day or night; the average maximum temperature, however, was 9° F. lower on wet days (74° F. on days without rain, 65° F. on days with rain).

MOONLIGHT.

Williams (1940) showed that for total insect catch over four years about twice as many insects were caught when there was no moon as when the moon was full and diminished the influence of the light trap. An analysis of the departures of the log. catch of aphides from a 5-day running mean showed no significant effect due to the phases of the moon. This is possibly because in the four lunar periods under consideration heat waves occurred about full moon, making the period distinctly warmer than at no moon.

SUNSHINE.

Day temperature and sunshine are highly correlated, and whereas the regression of log. catch on hours of sunshine, uncorrected for length of day, gave a co-efficient of $+0.032 \pm 0.011$, significant at 1 per cent., a regression analysis of log. catch on maximum temperature and hours of sunshine showed that there was no independent effect of illumination.

WIND.

Wind records from a Dines Anemograph, located at 70 feet from the ground, on the roof of the laboratory, about 340 yards to the east of the trap, have been examined and the average wind speeds determined for the four periods: (a) noon to one hour before sunset (day wind); (b) 3-2 hours before sunset (evening wind); (c) one hour before sunset; (d) during the night. These were placed in one of five groups—(1) dead calm; (2) 0-2 m.p.h.; (3) 2-5 m.p.h.; (4) 5-10 m.p.h.; (5) over 10 m.p.h.

TABLE 7.

Mean departure of log. catch and, in brackets, the number of nights in each wind group.

Wind group	1	2	3	4	5
(a) Wind from noon to one hour before sunset	+0.454 (5)	+0.162 (5)	+0.280 (25)	+0.088 (39)	-0.260 (46)
(b) Wind 3-2 hours before sunset	+0.297 (15)	+0.142 (7)	+0.246 (25)	+0.018 (34)	-0.274 (39)
(c) Wind one hour before sunset	+0.258 (41)	+0.097 (22)	+0.185 (14)	-0.289 (24)	-0.358 (19)
(d) Wind during the night	+0.264 (54)	-0.095 (13)	-0.155 (22)	-0.248 (26)	-0.382 (5)

The number of days or nights in each group for the four periods is given in Table 7. The nights and the single hours before sunset were usually much calmer than the days. Thus there were 67 nights in groups 1+2 and 31 in groups 4+5, compared with 10 days in groups 1+2 and 85 in groups 4+5.

The method of analysis consisted in placing in the correct wind group the departure of the log. catch from a 21-day running mean of the log. catches for each of the nights and finding the average catch departure for all nights in that category. The results are given in Table 7.

Regressions of log. catch on the three winds (a), (b) and (d) gave results as follows :

	Regression coefficients	Significant at
(a) Day wind	-0.201 ± 0.043	0.1%
(b) Evening wind	-0.152 ± 0.035	0.1%
(d) Night wind	-0.168 ± 0.034	0.1%

A regression analysis of log. catch on these three winds and maximum temperature indicated that day or evening wind had a much greater effect on the catch than had the wind during the night, and that of the first two the day wind had the more significant effect. The same conclusion was evident when the winds were considered in pairs.

WIND DIRECTION.

Table 8 shows the averages of the log. catch departures from the mean placed in groups according to the wind direction during the afternoons before the catch, and the average wind force (based on groups 1-5) in each direction.

TABLE 8.

Average departures of log. catch from the mean on days with different wind directions.

	NW.	N.	NE.	E.	S.E.	S.	SW.	W.
Departure from mean	+0.187	+0.128	+0.136	+0.158	+0.373	-0.338	-0.155	-0.176
Number of days	13	12	20	13	4	13	17	22
Mean wind force (group) ...	3.5	3.8	4.3	4.0	4.5	4.2	4.4	4.1

These directions were placed in two groups according to whether they had a positive or negative departure from the mean, and the average wind speed, maximum temperature and dew point were determined for the days in each group. (See Table 9.)

TABLE 9.

Wind direction ...	NW., N., NE., E., SE.	S., SW., W.
Average log. catch departure ...	$+0.165 \pm 0.034$	-0.210 ± 0.031
„ wind speed (group) ...	4.0	4.2
„ maximum temperature ...	71° F.	70° F.
„ dew point, 21.00 hrs. ...	53° F.	53° F.

The departures from mean are significant, and can hardly be accounted for by the very slight average differences between the other weather factors in the two groups.

A regression of log. catch on wind direction was calculated, using the sines of the angles from north and east respectively as values for the different directions. This gave a fit of log. catch on direction with a mean square of 1.469 and error of 0.280, which is significant at 5 per cent.

BAROMETRIC PRESSURE.

Following Williams' method, the nights of the months June to September, 1935, were divided into nine categories according to whether the barometer was, on the one hand, rising, steady or falling; and on the other hand, high, medium or low. Medium barometer was taken to be between 29.9 and 30.2 inches. The barometer reading was that at midnight, taken from the chart of a recording barograph. The departure of the log. catch from a 21-day running mean was entered for each night in its proper category, and the average departure for each category for the four months combined was thus obtained. Table 10 shows the results expressed as departures from the mean and as percentages of the mean. The number of nights in each category is given also.

TABLE 10.

Departure of log. catch of aphides from normal under various barometric conditions, June-September, 1935.

(The upper figure is the number of nights in the category, the middle figure is the departure from the mean, and the lower the percentage of the mean.)

Barometer	Rising	Steady	Falling	
High	13 +0.261 182%	16 +0.185 153%	15 -0.036 92%	44 +0.132 136%
Medium	21 -0.115 77%	12 +0.346 222%	21 -0.048 90%	54 +0.014 103%
Low	9 -0.146 71%	4 -0.303 50%	9 -0.313 49%	22 -0.243 57%
	43 -0.007 98%	32 +0.184 153%	45 -0.097 80%	

These results are in general agreement with those obtained by Williams (1940) for the whole insect catch over four summers. Above normal catches were obtained when the barometer was high, about normal when it was medium and below normal when low. The catch was below normal, however, when the barometer was high but falling: this phenomenon was noted also by Williams. The same tendency is noticed when the records are further analysed by dividing the actual barometer

readings into five groups, *i.e.*, 29.3-29.5, 29.6-29.8, 29.9-30.1, 30.2-30.4, 30.5-30.7 inches—and determining the mean departure of the log. catch from the normal for all the nights with each of these barometer levels (see Table 11).

TABLE 11.

Barometer level at midnight	Number of occurrences	Mean log. catch departure
29.3-29.5	6	-0.328
29.6-29.8	14	-0.236
29.9-30.1	51	-0.015
30.2-30.4	45	+0.072
30.5-30.7	4	+1.088

The regression coefficient for pressure was $+0.203 \pm 0.054$, significant at 0.1 per cent. It is unlikely that pressure would have exerted an influence as great as is suggested by the above figures. When the barometric pressure is high in summer the temperature is usually high, and it seemed probable that the apparent effect of pressure on catch was caused by other associated factors. A regression analysis of log. catch on pressure and maximum temperature showed this to be so.

ANALYSIS OF SEVERAL FACTORS SIMULTANEOUSLY.

The more important factors which might have affected the catch have been examined separately in the previous paragraphs; some were shown to have had no significant effect, others to have had an apparent effect because of their correlation with other factors. Maximum temperature, wind force and wind direction of the day previous to the catch and the evening dew point were shown to have had significant effects. A regression analysis of log. catch on these four factors showed that each remained significant when considered in conjunction with the others. The regression equation was :

$$\delta(\log_{10} y) = 0.029 \delta t + 0.023 \delta h - 0.158 \delta w + 0.061 \delta(\sin d) + 0.227 \delta(\cos d)$$

where y = log. catch

t = maximum temperature

h = dew point at 21.00 hrs.

w = day wind force

d = day wind direction (d° from north)

$$\text{Thus } \frac{\delta y}{y} = 0.066 \delta t + 0.052 \delta h - 0.364 \delta w + 0.140 \delta(\sin d) + 0.523 \delta(\cos d)$$

From this equation it was calculated that the percentage change in catch per 1° F. rise in maximum temperature (other factors being constant) was +7 per cent.; the change per 1° F. rise in dew point was +5 per cent.; an increase from one wind group to the next reduced the

catch by 36 per cent. The most favourable wind direction was 15° east of north. The effect of a change of wind direction from the most unfavourable direction (15° west of south) to the most favourable (the other factors being constant) was to multiply the catch by 3. It is worthy of note that the town of Harpenden lies about half a mile to the N.N.E. of the trap. Also a large area of allotments was close at hand to the north-east and east. These two areas might be presumed to have had large concentrations of aphides and might have been the cause of the directional effect.

This is the best estimate that can be made of the effect of the weather factors. It is possible that a slightly different equation could have been formed equally satisfactorily with weather factors measured at slightly different times—e.g., by taking mean temperature instead of maximum.

DISCUSSION.

Davies (1935, 1936), from laboratory experiments, found that the optimum conditions for flight of *Myzus persicae* Sulzer were a temperature above 70° F., a relative humidity below 70 per cent. and a wind velocity below 4 m.p.h. Thomas and Vevai (1940), by combining Davies' results with their analysis of five seasons' trapping of aphides, suggested slight modifications of the above conditions for flight of aphides in the field—namely, temperature above 70° F., with a difference between maximum and minimum of more than 12° F., relative humidity below 80 per cent.; wind velocity below 5 m.p.h. In experiments with *Capitophorus fragariae* Theobald, Greenslade (1941) found that flights took place at temperatures of 61° F. and above. These conditions could rarely have been fulfilled during the periods of operation of the light trap. The minimum temperature during the summer months at Rothamsted during the four years 1933 to 1936 varied between 40° F. and 60° F. with the monthly means between 45° F. and 55° F. The humidity of the air near the ground at night is high, averaging 85–90 per cent. in the summer months. Because of the low temperatures and high humidities it has often been assumed, and some workers have stated, that flying does not take place at night. For example, Profft (1939), although he stated that the reaction of flying aphides to the onset of darkness was unknown, concluded that the insects probably alighted for the night on any green plant, provided that the air currents permitted them to land. From Davies' data on temperatures and humidity, they would be expected to settle after sunset. That this assumption is unjustified is clearly shown by the fact that aphides are caught in the light trap. If aphides ceased flying with nightfall, the catches would have been concentrated in the early periods of the night; actually the catches were fairly evenly distributed throughout the night in July and August, and on many nights the numbers increased in the later periods.

The aphides might have taken to flight during the previous day and remained in the air, or they might have flown from their hosts during the night. During the day they may have been subject to strong winds or thermal convection currents and carried long distances involuntarily. At night, however, the wind normally dies down and

thermal convection currents almost cease, so that they would have to fly voluntarily during most nights. Because of the correlation of catch with the weather of the previous day it seems reasonable to assume that the aphides caught did start to fly before nightfall, had flown or been carried by eddies and thermal convection currents, then at night found themselves under calm conditions which would enable them to undertake voluntary flight. However, this necessitates the postulate that aphides can fly actively for six to ten hours, unless they had been falling from considerable heights to which they had been carried during the day. Glick (1939) stated that insects which are in the upper air during the day tend to be brought down at night with the descending cool air currents, or because of the failure of upward convection currents. In the lower atmosphere the closer to the ground on calm nights, the colder the air, and it may be that the aphides were deterred from landing by this cold stratum. That some insects tend to fly in definite air strata at night was shown by Wellington (1944) when collecting *Culex* spp. at height intervals up to sixty feet. On nights when the catch increased rapidly during a particular period a swarm of aphides from a distant source might have been passing and have been attracted to the lamp.

On the other hand, the catches may have consisted of local specimens only. Conditions for aphid flight might be suitable in certain localities on a night when flight would be inhibited in the open country. Wellington (1945) pointed out that slow convection currents of warmer air are produced after sunset over isolated dark-coloured built-up areas and clumps of trees. Geiger (1927) reported that temperature inversions did not occur in a walled garden. Thus the orchard to the north-west of the trap and the town of Harpenden, as well as the lamp of the trap itself, might have set up small thermal convection currents and have encouraged aphides to fly. Aphides are positively phototropic, but little appears to be known of their reaction to different light intensities. Davies (1935) and Greenslade (1941) both stated that light intensity had an effect on flight apart from that of temperature. To what extent aphides would fly at night if factors other than illumination were favourable is not known.

It has been noted that the results of the analysis support those of Freeman, and in the middle ranges of humidity, conflict with those of Davies. It would appear that in the field, an increase of water vapour in the air (at least to a dew point of 64° F.) favours fighting for aphides in general. Davies, in his experiments with *Myzus persicae*, found that fighting increased with decreasing relative humidity when the temperature was kept constant. However, a rise in dew point is usually accompanied by a rise in temperature, and although the analysis showed that dew point had a significant effect on catch apart from maximum temperature it is not clear how the absolute humidity (as measured by dew point) could affect the activity of insects.

The present analysis has shown without doubt that aphides fly throughout the night and has indicated the weather factors which influence night flight. Nothing is known about the species caught in the light trap, not even whether the catch consisted of many or few species.

Before the general value of the correlations shown by this work can be appreciated, many more experiments will be needed on the factors influencing flight in different species.

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